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BULLETIN OF THE TORREY BOTANICAL CLUB
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PRODUCTION OF PENICILLIN ON NATURAL MEDIA

D. PERLMAN

The production of penicillin on media which included natural materials as sources of nitrogen and other factors has received considerable attention during the past few years. Moyer and Coghill (20, 21) have reported studies where the inclusion of cornsteep liquor in a lactose–salts medium was found to increase the yields of penicillin markedly. Bowden and Peterson (3) have noted that under the conditions of their experiments "no satisfactory substitute for cornsteep liquor has been found," although the addition of other materials to the cornsteep liquor–lactose–salts medium resulted in some increase in antibiotic activity. More recently Cook and his associates (6, 7, 8) have observed that the addition of extracts of dried peas to a carbohydrate–salts medium increased the yields of penicillin in surface culture, and that gelatine and other factors may partially replace the pea extract. As the chemistry of the penicillins became known it was concurrently observed that the types of penicillin produced depend in part on the presence of certain compounds present in the medium which act as precursors leading to the production of penicillin G (benzylpenicillin) or other types (1, 4, 13, 19). Foster and his coworkers (9, 10) have reported that cottonseed meal and other materials may completely or partially replace cornsteep liquor in the medium without considerable reduction in penicillin yield (antibiotic potency). With cottonseed meal it was noted (10) that equivalent yields of penicillin were obtained with or without the addition of a penicillin G precursor to the medium (of the general types mentioned in 13 and 23), while much lower yields were obtained on the cornsteep liquor medium when the precursor was not added.

The studies reported here indicate that several other proteinaceous materials may be substituted for the cornsteep liquor in media for the production of penicillin without marked change in penicillin yield. When these studies were completed early in 1946 the elegant analytical methods for the quantitative and qualitative estimation of penicillin in fermentation broths recently described by Prof. Johnson (16) were not available and thus it is not known whether the same penicillins are produced on all these media. From the recent report by Jarvis and Johnson (14) on penicillin production on synthetic media it appears probable that the bulk of the antibiotic activity on a natural medium supplemented with a penicillin G precursor will be penicillin G if the Wisconsin Q_{176} strain of *Penicillium*

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chrysogenum is used. It is interesting to note that the potencies mentioned (in the following experiments) are of the order of 0.5 mg. per ml. or approximately 1 per cent of the total solids present in the crude broth, a purity related by Chain (5) as equivalent to that used in the early therapeutic tests.

Methods. The analytical methods used in these studies were in the main those described by Koffler and associates (17). The culture of *P. chrysogenum* Wis. Q_{176} (described by Backus et al., 2) obtained from Prof. M. P. Backus was cultured on the medium mentioned by Gailey and others (11) as being optimal for *P. chrysogenum* Demerec X 1612. The fermentations were carried out at 22–24° C. in cotton plugged 250 ml. Erlenmeyer flasks containing 80 ml. of medium. After inoculation these flasks were placed on rotary shaking machines (220 rpm) mentioned by Foster and others (9). A vegetative inoculum was used in all experiments, and was prepared (unless otherwise indicated) by inoculating flasks containing a medium consisting of the indicated nitrogenous material (at 2 per cent solids concentration) and 2 per cent glucose (or other carbohydrate as indicated) with approximately 1 ml. of a spore suspension prepared as described by Gailey and others (11). After approximately 48 hrs. incubation on the shaking machines ca. 2 ml. of the vegetative growth (resembling paper pulp) was added to each of the fermentation flasks. There were usually three or more replicate flasks of each experiment. The flasks were sampled daily after the third day of incubation until assays on two consecutive days had indicated that a maximum yield had been reached. Each flask was sampled and assayed individually, and the results from replicate flasks were averaged. In the results presented in table 3 duplicate flasks were removed at the end of the indicated fermentation period and the contents were pooled before analysis. Control flasks containing cornsteep liquor–lactose medium were included with each group of fermentations to check for peculiarities in behavior of the fermentations that might be attributed to cultural abnormalities. Gailey and his associates (11) have reported that the penicillin yields may vary considerably with a given culture on a given medium, and in the course of these experiments the yields ranged from 1350 U. per ml. to 950 U. per ml. on the cornsteep liquor medium. Accordingly any yield in the vicinity of 1000 U. per ml. has been considered as good. Unless otherwise indicated the medium used in all fermentations contained (per liter): calcium carbonate, 10 g.; soybean oil, 3.2 ml.; and tap water q.s. one liter. All flasks were autoclaved at 120° C for 20 minutes. The other ingredients of the media were obtained from various commercial sources. The penicillin G precursor added was similar to those mentioned in the literature (1, 12, 13, 18, 23).

Experiments. The results obtained when a number of naturally occurring proteinaceous materials were substituted for the cornsteep liquor in the medium mentioned above are summarized in table 1. Several concentrations of each substance were tested as indicated, in media with and without the added penicillin G precursor. While considerable data were collected in these experiments only the maximum yields of antibiotic activity are noted in order to make the comparisons clear. In most cases when the concentration of proteinaceous material was increased to 40 grams per liter the resulting mycelial growth was so voluminous that no doubt the aeration and agitation were impaired and consequently the same aerobic conditions did not exist in these flasks that were obtained in the others containing less of these materials. This is thought to account for the lowered penicillin yields found in certain cases, and undoubtedly under higher and more efficient aeration the yields would be higher as deduced from the results obtained by Bowden and Peterson (3). It will be seen that with certain materials including yeast extract very poor yields were obtained. In these fermentations the pH rose quickly to 7.8 and shortly thereafter to 8.5 indicating that perhaps autolysis was occurring, an observation confirmed by the odor of ammonia which has been associated with the autolytic phase of the fermentation by Koffler and others (17) who reported that little penicillin is usually found under these conditions.

The previous history of the inoculum was thought to have some importance in the results obtained by Foster and his coworkers (10). The importance of this factor in these studies is summarized in table 2 where the data obtained in several experiments are collected. The carbohydrate source present in the inoculum medium was varied between lactose, mannitol, starch, inulin, sorbose, xylose, and glucose. These have been used in previous studies.[1] A number of proteinaceous materials included cornsteep liquor, cottonseed meal, linseed meal, and menhaden meal. The carbohydrate source in the inoculum medium seems to have some effect, but not as much as the nitrogen source. For example, if the inoculum was grown on a menhaden meal—glucose medium lower yields were obtained during the fermentation than if it were grown on a cornsteep liquor—glucose medium. Thus, while faster growth was observed on the cottonseed medium (Foster et al., 10), it would not be the best inoculum to use to inoculate fermentation media containing other nitrogen sources.

A considerable number of studies have been reported on the chemical changes occurring during the penicillin fermentation (reviewed by Johnson, 15). Some of the data collected during these experiments are presented in table 3. It will be seen that the penicillin yields on the three

[1] D. Perlman, Ph.D. Thesis, University of Wisconsin, 1945.

TABLE 1. *Production of Penicillin on Natural Media.*

Substance substituted for cornsteep liquor[a]	g./l	Maximum penicillin production	
		Without precursor U./ml.	With precursor U./ml.
Cornsteep liquor (solids)	20	650	1300
	30	580	1050
	40	400	800
Cottonseed oil meal	30	800	1200
	40	1000	1160
Linseed oil meal	20	700	1035
	40	635	1100
	60	.....	570
Coconut oil meal	60	450	1150
	90	500	810
	120	300	680
Sardine meal	10	150	610
	20	400	900
	30	575	1130
Rape seed oil meal	10	150	340
	20	180	450
	30	285	515
	60	730	705
	90	335	615
Peanut oil meal	10	300	710
	20	600	630
	30	950	900
	40	1050	1350
Mustard flour	30	650	980
	40	590	1060
Dried peas (split)	20	345	305
	30	280	250
	40	250	240
Dried beet crowns	50	.....	90
	100	.....	90
	150	.....	75
Yeast extract (Difco)	30	.....	45
	60	.....	40
	90	.....	55
Peptone (Bacto)	30	400	750
	60	50	90
	90	45	90
Soybean oil meal (expeller)	20	305	1030
	40	170	930
Castor bean meal	20	780	390
	40	460	430
Menhaden meal	20	780	390
	40	460	430

TABLE 1 (*Cont.*)

Substance substituted for cornsteep liquor[a]	g./l	Maximum penicillin production	
		Without precursor U./ml.	With precursor U./ml.
Fish meal (mixed)	20	830	430
	40	540	790
Poppy seeds	20	180	275
	30	270	320
	40	265	440

[a] Other ingredients included 30 g. lactose and 1 g. penicillin G precursor (where indicated), 3.2 ml. soybean oil, and 10 g. calcium carbonate per liter.

media are approximately equal, and that many of the changes found were the same in the three media. The pH did not rise as high in the cottonseed meal and linseed meal media as it did in the cornsteep liquor medium, but of course these materials did not contain the lactate present in the latter medium (Koffler et al., 17). The mycelium weights were greater on the cottonseed meal and linseed meal media than on the cornsteep liquor medium, but may have been incorrect since visual observation indicated that the meal was not completely disintegrated in those media until after the third and fourth days of the fermentation. The lactose fermentation in the linseed media was somewhat slower than in the other two media. Respiration measurements indicated that the oxygen demands were approximately the same on all three media. The nitrogen in solution (Kjeldahl) data were undoubtedly affected by the slow breakdown of the protein matter in the linseed and cottonseed meal media and are consequently incorrect. Cornsteep liquor is relatively high in inorganic phosphorus while the cottonseed meal and linseed meal are relatively low. However, a few determinations indicated that there was evidently enough phosphate present that some was found in the mycelium-free medium. Another observation indicated that the mold hydrolyzed the proteinaceous material fairly rapidly as indicated by the disappearance of the particles of meal, and also by the presence of soluble nitrogen in the solution during the fermentation, and a crude assay for extracellular proteinase indicated that, as might be expected, the extracellular proteinase production was highest in the media containing the unhydrolyzed protein.

Discussion. These few experiments have tended to confirm the reports by others (7, 10, 14) that penicillin production on cornsteep liquor containing media is not a result of something intrinsically special about this substance, since cottonseed meal, linseed oil meal, castor bean oil meal, and many other proteinaceous materials can be substituted for the cornsteep

liquor without reduction in penicillin yields. It is probable that the advantage of cornsteep liquor may be associated with its phenylalanine and phenylethylamine constituents (19) and the phenylalanine content of other products is as high as that found in cornsteep liquor. It is interesting to note that with a number of materials the yields of penicillin with and without added penicillin G precursor were approximately equal, e.g. media prepared with cottonseed meal, rape seed oil meal, peanut oil meal, and dried peas. Whether or not the same penicillins were produced under these conditions was not determined. According to Johnson (16) this organism produces mainly those penicillins with aliphatic side chains in synthetic media (14), and penicillin G production is associated with the presence of a phenyl acetyl derivative, or a substance yielding phenylacetyl derivatives during the fermentation.

Under the conditions of these experiments several materials which have previously been reported by others as satisfactory for inclusion in media for the production of penicillin have not yielded very satisfactory results, e.g. dried peas. On the other hand Ulkin (22) reported that peptone was definitely unsatisfactory, and in these experiments it was fairly good as a replacement for the cornsteep liquor in media supplemented with the penicillin G precursor. Undoubtedly the great differences in experimental conditions account for the disagreement in results between these different laboratories.

The experiments on the effect of history of inoculum on penicillin production are somewhat inconclusive. Evidently under certain conditions the

TABLE 2. *Effect of Inoculum Medium Composition on Penicillin Production.*

A. Nitrogen source Inoculum medium[a]	Fermentation medium[b]	Maximum penicillin production U./ml.
Cornsteep liquor	Cornsteep liquor	880
	Linseed oil meal	750
	Cottonseed oil meal	775
	Menhaden meal	570
Cottonseed meal	Cornsteep liquor	730
	Linseed oil meal	540
	Cottonseed oil meal	830
	Menhaden meal	585
Linseed oil meal	Cornsteep liquor	865
	Linseed oil meal	790
	Cottonseed meal	740
	Menhaden meal	460
Menhaden meal	Cornsteep liquor	350
	Linseed oil meal	600
	Cottonseed meal	900
	Menhaden meal	630

TABLE 2.—*Continued*

B. Carbohydrate source. Inoculum medium carbohydrate[c]	Fermentation medium[d]	Maximum penicillin production U./ml.
None	Lactose—cottonseed meal	910
	Lactose—peanut oil meal	765
	Mannitol—peanut oil meal	765
Glucose	Lactose—cottonseed meal	850
	Lactose—peanut oil meal	735
	Mannitol—peanut oil meal	800
Lactose	Lactose—cottonseed meal	960
	Lactose—peanut oil meal	695
	Mannitol—peanut oil meal	700
Mannitol	Lactose—cottonseed meal	835
	Lactose—peanut oil meal	760
	Mannitol—peanut oil meal	725
Starch	Lactose—cottonseed meal	950
Inulin	Lactose—cottonseed meal	1055
Sorbose	Lactose—peanut oil meal	880
	Mannitol—peanut oil meal	825
Xylose	Lactose—peanut oil meal	660
	Mannitol—peanut oil meal	860

[a] Cornsteep liquor: 20 g. cornsteep liquor solids; 20 g. glucose; tap water q.s. 1 liter.
Linseed oil meal: 20 g. linseed oil meal; 20 g. glucose; tap water q.s. 1 liter.
Cottonseed meal: 20 g. cottonseed meal; 20 g. glucose; tap water q.s. 1 liter.
Menhaden meal: 20 g. menhaden meal; 20 g. glucose; tap water q.s. 1 liter.

[b] Cornsteep liquor: 20 g. cornsteep liquor solids; 30 g. lactose; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.
Linseed oil meal: 40 g. linseed oil meal; 30 g. lactose; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.
Cottonseed meal: 30 g. cottonseed meal; 30 g. lactose; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.
Menhaden meal: 30 g. menhaden meal; 30 g. lactose; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter; 10 g. calcium carbonate.

[c] Inoculum medium: 20 g. indicated carbohydrate; 20 nitrogenous material (as in fermentation medium); tap water q.s. 1 liter.

[d] Fermentation medium: 30 g. lactose or mannitol as indicated; 40 g. cottonseed meal or peanut oil meal as indicated; 10 g. calcium carbonate; 3.2 ml. soybean oil; tap water q.s. 1 liter. (Note: no penicillin G precursor was added to these media.)

addition of no carbohydrate to the inoculum medium is better than other combinations. The nitrogenous material present in the inoculum phase is perhaps much more important than the carbohydrate in determining the penicillin yields in the fermentation medium, and evidently care should be taken to make sure that certain combinations are not used.

The few studies on chemical changes occurring during the fermentation tend to indicate that the same general changes occur in media containing the cottonseed meal and linseed oil meal instead of the cornsteep liquor. Perhaps under other fermentation conditions significant differences

would be found between the changes occurring during the fermentation of the three media, and the standardization of procedure has limited the number of satisfactory replacements for the cornsteep liquor. It is not

TABLE 3. *Chemical Changes Occurring During the Fermentation of Natural Media.*

Medium[a]	Duration of fermentation					
	0 day	2 days	3 days	4 days	5 days	6 days
Penicillin Production (U./ml.)						
Cornsteep liquor	.....	690	1100	1450	1170	1020
Cottonseed meal	.....	550	980	1350	1190	900
Linseed oil meal	.....	400	900	1300	1140	1150
pH						
Cornsteep liquor	6.70	7.20	7.25	7.45	8.25	8.45
Cottonseed meal	6.35	6.80	7.15	7.70	7.35	7.55
Linseed oil meal	7.00	7.15	7.20	7.05	7.40	7.60
Mycelium Weight (mg./ml.)						
Cornsteep liquor	.....	24	26	22	23	19
Cottonseed meal	.....	.....	30	33	30	31
Linseed oil meal	.....	.....	.....	33	30	29
Lactose (mg./ml.)						
Cornsteep liquor	29	16	9	3	4	3
Cottonseed meal	31	18	11	6	7	5
Linseed oil meal	27	20	18	10	7	3
Oxygen Demand (Q_{O_2}/ml.)						
Cornsteep liquor	.....	84	75	62	55	38
Cottonseed meal	.....	.....	65	68	50	48
Linseed oil meal	.....	.....	.....	58	60	50
Nitrogen (Kjeldahl) in Solution (mg./ml.)						
Cornsteep liquor	2.25	1.24	1.04	1.39	1.48	1.58
Cottonseed meal	1.60	1.75	1.00	0.90	0.70	1.10
Linseed oil meal	1.90	1.60	1.05	0.95	0.80	0.90

[a] Composition of media: *Cornsteep liquor:* 20 g. cornsteep liquor solids; 30 g. lactose; 10 g. calcium carbonate; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter.

Cottonseed meal: 30 g. cottonseed meal; 30 g. lactose; 10 g. calcium carbonate; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter.

Linseed oil meal: 40 g. linseed oil meal; 30 g. lactose; 10 g. calcium carbonate; 1 g. penicillin G precursor; 3.2 ml. soybean oil; tap water q.s. 1 liter.

surprising that synthetic media based in part on the composition of cornsteep liquor have been found to give nearly as high penicillin yields as are obtained with the cornsteep liquor medium (14).

The author wishes to express his appreciation to Dr. P. K. Frolich (now Director of Research, Merck & Co., Inc.) for permission to publish the above results.

SUMMARY

A number of natural materials have been found to replace cornsteep liquor in the penicillin production medium. These include cottonseed meal, linseed oil meal, coconut oil meal, sardine meal, peanut oil meal, mustard flour, soybean oil meal, and perhaps castor bean meal. The composition of the inoculum medium has a pronounced effect on the fermentation. The gross chemical changes occurring during the fermentation of media prepared with cornsteep liquor, linseed oil meal, and cottonseed oil meal are quite similar.

PRINCETON, NEW JERSEY.

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ATKINSIA GEN. NOV., THESPESIA, AND RELATED WEST INDIAN GENERA OF THE MALVACEAE[1]

RICHARD A. HOWARD

In a recent issue of the New Phytologist (**46**: 123–141. 1947) J. B. Hutchinson has published a study entitled "Notes on the classification and distribution of genera related to *Gossypium*." His paper concerns a group of genera suggested as a division of the Hibisceae of the Malvaceae, with "rounded, compressed or turbinate seeds and with the styles usually joined and clavate and only rarely free or capitate." In his paper, Hutchinson has placed the West Indian genera, *Montezuma* Sessé & Mociño, *Maga* Urban, and *Armouria* Lewton, in the synonymy of the genus *Thespesia* Solander, including them by expanding the generic limits of the genus *Thespesia*. I can not agree with Hutchinson's conclusions and in this paper will separate the native West Indian species from *Thespesia* and maintain them as species in monotypic endemic genera.

There are superficial similarities which hold the genera together in a general complex, but there are striking differences between the various species occurring in the West Indies which I feel Hutchinson does not evaluate properly. Certainly the circumscissile deciduous calyx of *Thespesia grandiflora* is strikingly different from anything else in the genus as characterized by Hutchinson. *Thespesia cubensis* is readily distinguished by the shortened leafless terminal spike of flowers, the short corolla exceeded by the staminal column, the persistent woody calyx, and the domatia in the axils of the primary veins. *Thespesia beata* is distinct with a loculicidally dehiscent capsule, lobed and densely pubescent leaves, and the calyx investing the mature capsule.

It is my opinion that these differences between many of the species of *Thespesia* as treated by Hutchinson are as great as or greater than the differences between other genera in his treatment of this division of the Hibisceae. Most of the genera of Hutchinson's treatment are small and readily characterized. I can see no reason for expanding the genus *Thespesia* to become a catch-basket. I therefore propose to follow the earlier treatments of Urban, Britton and Lewton and maintain the West Indian species, which Hutchinson calls *Thespesia grandiflora*, *T. cubensis*, and *T. beata*, as the type species of monotypic genera on the strength of the characters given in the key below.

In addition errors have crept into Hutchinson's work. He apparently did not see any herbarium material of *Thespesia cubensis* nor did he read

[1] Publication No. 4. Jounal Series from the Atkins Garden and Research Laboratory of Harvard University, Soledad, Cienfuegos, Cuba.

Urban's comments on this species (as *Maga cubensis*) published in Fedde Repert. Sp. Nov. **24**: 237 (1928). The original description of this species does not agree with the type specimen and this discrepancy was noted by Urban. It can be readily observed from the numerous collections of this species, in addition to the type collection, that the calyx is not circumscissile but woody and persistent. It was on the supposed character of a "circumscissile" calyx that Britton and Wilson placed the species in the genus *Maga* [= *Montezuma*] and this erroneous character is still used by Hutchinson to place *T. cubensis* in his key.

The material referred to as *Maga cubensis* by Britton and Wilson is a distinct species and can not be accommodated in *Thespesia* or *Montezuma*. A new genus is established for this species in the present paper.

Hutchinson also overlooked the genus *Ulbrichia* Urban, based on material collected by Ostenfeld on Beata Island near the Dominican Republic. The material is identical with that collected by Fairchild and Dorsett on the same island; which is the type of *Armouria beata* Lewton. Urban's new genus and species *Ulbrichia beatensis*, antedates *Armouria beata* by nine years.

After the endemic West Indian species have been removed from Hutchinson's amended *Thespesia*, the genus contains five species. The species typifying the genus, *T. populnea*, is a pantropical coastal weedy tree. The fruits are used medicinally throughout the tropics. The flowers are eaten for food and the tree itself is planted as a shade or ornamental tree. Its widespread use as a cultivated plant for coastal areas is a result of its tolerance to salt spray. Two species are found in Africa, *T. danis* Oliver and *T. Garckeana* F. Hoffm. I have not seen any material of *T. danis* and can find no elaboration of the original description and plate of the plant in flowering condition. Certainly the position of the bracteoles (Hook. Ic. **14**: *pl. 1336*. 1881) high on the calyx is unusual for *Thespesia*. A fourth species, *T. lampas* Cav. is widely used as an ornamental. It is reported as introduced into the Philippines, Java, and Jamaica. It is also reported from Ceylon and India, Burma, Siam, Indo-China, the Celebes, and Hawaii. It is probably native in India where it occurs as a forest shrub. *Thespesia lampas* has been considered distinct from *Thespesia* and was proposed as the type species of the genus *Azanza* by Alefeld (Bot. Zeit. **19**: 298. 1861). It has been accepted as a distinct genus by several recent authors. The last species left in Hutchinson's treatment is *Thespesia tomentosa* Presl. from Western Mexico, apparently known only from the original description. Standley does not mention this species in his *Trees and shrubs of Mexico*. *T. tomentosa* appears to be similar to *Ulbrichia beatensis* in its pubescence but has 8 bracteoles compared with 3 in *Ulbrichia*.

For a discussion of the problem of limitation of the genus *Thespesia* and for notes on the original description, see the article by Baker entitled "Notes on *Thespesia*" (Jour. Bot. **35**: 50–54. 1897).

Several morphological characters found generally in the Malvaceae and in this group of West Indian genera merit further comment. Frequently, in the Malvaceae, the calyx is pubescent on the inside as well as the outside. The genera considered in this paper have a cupular calyx usually truncate at the apex. The pubescence inside the calyx is very dense on all specimens I have seen, yet this character is not mentioned in most of the earlier descriptions. The pubescence consists of lepidote-stellate hair clusters with the free arms of the cluster often very long and giving the impression of a dense tomentum of individual hairs.

Urban paid considerable attention to the shape of the ovary and fruit and the number of locules in his generic descriptions. The ovary is 5-celled but usually only 3 or 4 of the locules will mature seeds. The other locules may be enlarged so that the fruit is symmetrical or the locules may be collapsed and not at all evident giving an asymmetrical fruit. The ovules are attached at the base and careful dissection will usually show the abortive seeds near the base of the fruit.

As is typical in many of the Malvaceae, punctate lines or dots are found on many parts of the plant in the species considered in this paper. The calyx is usually heavily black-dotted and at times the resinous material may exude in drying so that the fruiting calyx will be filled, around the capsule, with black resinous droplets. The petals may have numerous black lines or dots, associated with the veins or aggregated near the upper margin of the petal. The inner layers of the fruit may be filled with resin-bearing cells. Urban, after dissecting seeds, distinguished between several genera on the presence or absence of black dots in the cotyledons. I have examined most of the material cited by Urban plus many other specimens of all the species cited in this study and have found resin-bearing cells in the cotyledons of all seeds examined.

The author is grateful to the curators of the following herbaria for material examined in the course of this survey: Gray Herbarium (G), The New York Botanical Garden (NY), and the United States National Herbarium (US).

Calyx circumscissile in fruit; ovary glabrous; [seeds glabrous]. *Montezuma.*
Calyx persistent in fruit; ovary lepidote or lepidote-stellate.
  Calyx expanded in fruit, flat, recurved or undulate; [staminal column shorter than the corolla; capsule indehiscent;] seeds pubescent. *Thespesia.*
  Calyx cupular, enclosing the fruit, entire or broken; seeds glabrous.
    Calyx cupular, half investing the capsule, entire; staminal column shorter than the corolla; flowers solitary, axillary to the leaves; capsule loculicidally 5-valved. *Ulbrichia.*
    Calyx expanded and broken in fruit; staminal column exceeding the corolla [1.5–3 times as long]; flowers in shortened terminal leafless spikes; capsule indehiscent. *Atkinsia.*

MONTEZUMA Sessé & Moc.; DC. Prodr. **1**: 477. 1824.

Maga Urban, Symb. Ant. **7**: 281. 1912.

Trees. Leaves alternate, petiolate, entire or slightly undulate, broadly ovate, cordate. Stipules small, deciduous. Flowers solitary in the axils of leaves, on simple peduncles. Involucre of 3 small, linear, deciduous bracts. Calyx subcampanulate truncate, circumscissile at the base after flowering, deciduous. Petals 5, large, united at the base. Staminal column united at the base with the corolla, scarcely as long as the petals. Stigmas united, clavate. Ovary sessile, glabrous, 5-celled, ovules about 5 in each locule. Capsule fleshy, becoming woody when dry, thick, indehiscent. Seeds glabrous, cotyledons black-punctate.

MONTEZUMA GRANDIFLORA (DC) Urb.; Urb. & Helwig, Repert Sp. Nov. **24**: 238. 1928. (Figs. 1–6). *Thespesia grandiflora* DC. Prodr. **1**: 456. 1824. *Maga grandiflora* Urb. Symb. Ant. **7**: 281. 1912. *Montezuma speciosissima* Sessé & Moc.; DC. Prodr. **1**: 477. 1824. Urb. Notizbl. **7**: 543. 1921.

Tree to 15 m. tall; young branches stout, lepidote-stellate-pubescent; stipules linear-subulate, 3–4 mm. long, deciduous; leaves orbicular-ovate, 5–25 cm. long (4) 8–19 cm. broad, apex acuminate or acute, base cordate rarely subtruncate, the lobes often overlapping, margin entire to undulate, sparsely lepidote-stellate on both sides when young, especially at the base of the blade; palmately 5–7-nerved; petioles 3–18 cm. long, lepidote-stellate; peduncles 6–25 cm. long, lepidote-stellate, bracteoles 3, linear, 1.8 cm. long, 1.5 mm. broad, caducous; calyx cyathiform or subcampanulate, 1.7–2.5 cm. long, 1.5–2 cm. diameter in flower, truncate at the apex, minutely lepidote-stellate outside, densely long-tomentose inside, the hairs usually clustered; petals obliquely triangular-obovate, 7–11 cm. long, 5–7.5 cm. broad, deep rose shading to crimson inside, orange or tan outside, with black dots or lines along the veins in the center of the petal, densely lepidote-stellate to tomentose outside, glabrous inside; staminal column 4.5–7 cm. long, shorter to rarely equalling the petals, column irregularly dentate at the apex, filaments 2–4 mm. long, usually in pairs and arranged in 5 vertical rows; ovary sessile, ovate to conical, glabrous, 5-loculed, ovules about 5 in each locule; capsule ovoid, 3–5 cm. diameter, apparently fleshy when fresh becoming woody when dry, walls thick; seeds 3–5 in each locule, obovoid, 1.2–1.3 cm. long, 7–9 mm. broad, glabrous, black, cotyledons black dotted.

Illustrations: A. DC. Calq. Diss. Fl. Mex. Moc. & Sessé *pl. 1.* 1874.

PUERTO RICO: San German, at Lajas-arriba, *Sintenis 3957* (G, NY, US), in fruit in Sept.; Laguna Tortuguero, *Britton, Cowell & Brown 3835* (G, NY, US), in flower in Feb.; Vega Baja, *Stevens 1899* (NY), in fruit in Jan.; *Britton 8592* (NY), in flower in Feb.; Manatí, *Stevensen 1955* (NY, US), in flower in June; Arecibo, *Hess & Stevens 5065* (NY), in fruit in Nov.; Rio Nuevo, *Britton, Britton & Boynton, 8158* (NY), in flower in Jan.; Canovanas, *Holdridge 234* (NY), in flower in March; Bayamon, *Britton & Britton 8987* (NY), in flower in Mar.; *Britton, Britton & Boynton, 8454* (NY), in sterile condition in Mar.; *Sintenis 1050* (G, US, sheets labelled Type Collection), in flower in April; Pena de las Cuevas, near Juana Diaz, *Britton & Marble 2291* (NY, US), in flower in March; Yauco, *Sargent 504* (US), in flower in March; Dorada, *Miller 1616* (US), in flower in March. CUBA: Las Villas: Soledad, *Jack 8489* (NY), sterile condition in Feb.; *Howard 4114* (G), in flower in June. Both collections from cultivated material.

Local names: Maga, Magar, Magas (fide Urban).

The plants are native in Puerto Rico growing in woods and on hillsides away from the coast. The tree is commonly planted as a roadside tree for

FIGS. 1–6. *Montezuma grandiflora* (*Holdridge 234*). FIG. 1. Habit. Pubescence omitted; note fruiting pedicel after capsule has fallen. FIG. 2. View of glabrous seed. FIG. 3. Circumscissile calyx and young fruiting pedicel. FIG. 4. Longitudinal section of fruit. FIG. 5. Mature fruit. FIG. 6. Cross-section of mature fruit showing plump seeds in four locules. All drawings × ½.

shade or as an ornamental for its showy flowers. The wood is hard and durable and valued for furniture or for posts.

The collections of *Sintenis 1050* (G, US) have been annotated "Type collection", by some earlier worker. The original description by DeCandolle refers to "Hibiscus grandiflora Juss. ined." and no specimens were cited. Since the Sintenis material is generally widely distributed, it seems proper to designate this collection as the type.

Urban established the genus *Maga* to accommodate *Thespesia grandiflora DC. Montezuma* Sessé & Moc. is an older name for the genus. Urban considered the circumscissile calyx which is deciduous, the glabrous seeds, a 3–4 locular ovary and the lack of black punctate dots in the cotyledons as generic characters. The first two, that is, circumscissile and deciduous calyx (figs. 1, 3), and glabrous seeds (fig. 2) may be maintained as generic characters. The ovary in all of the material I have examined has 5 locules in the flower but seeds may be developed in only 3 or 4 (fig. 6) of these or in all five locules. The cotyledons of the embryo do have black punctate dots although these are not as abundant as in species of *Thespesia*. Thus the latter two characters cannot be used to distinguish between *Montezuma* and *Thespesia*.

THESPESIA Soland.; Correa, Ann. Mus. Paris **9**: 290. 1807. *pl. 8, f. 2.*

Shrubs or trees. Leaves alternate, entire, usually cordate or broadly 3–5-lobed; stipules linear. Flowers solitary and axillary on simple or jointed pedicels. Involucre of 3–15 bracteoles, these free, ovate, acute or acuminate, linear or filiform, persistent or caducous. Calyx subhemispheric, truncate or nearly so, persistent, expanding and becoming repand and undulate in fruit. Petals 5, united at the base. Staminal column shorter than the corolla, 5-toothed at the apex, filaments free from or united with the column. Ovary sessile, 5-celled, ovules 3 or 4 in each locule. Capsule woody or leathery, 3–5-celled, indehiscent. Seeds obovoid, compressed, pubescent, cotyledons black-punctate.

THESPESIA POPULNEA (L) Soland.; Correa, Ann. Mus. Paris **9**: 290. 1807. *Hibiscus populneus* L. Sp. Pl. 694. 1753. *Malvaviscus populneus* Gaertn. Fruct. **2**: 253. *pl. 135.* 1791.

Shrub or small tree 1–20 m. tall; young branches lepidote-stellate; stipules linear, 5–10 mm. long, early caducous; leaves ovate-orbicular to ovate-acuminate, 5–15 cm. long, 3–11 cm. broad, apex acuminate, base cordate, margin undulate, sparsely lepidote-stellate on both surfaces; palmately 5-nerved, occasionally with small domatia harboring scale insects in the axils; petioles 4–8 cm. long; flowers solitary, axillary, peduncles 2–4 cm. long; bracteoles 3, free, linear or acute, 1–1.4 cm. long, 2–3 mm. broad at the base, lepidote-stellate-pubescent; calyx subhemispheric, 1 cm. high, 1.5 cm. diameter, truncate or with 5 minute teeth, densely lepidote-stellate outside, pubescence inside the calyx of lepidote-stellate clusters with the free arms of the hairs to 4 mm. long, the pubescence appearing as tomentose; petals 4–7 cm. long, 3–5 cm. broad, yellow with a darker base changing in age to flesh color, orange, red or purple, numerous black punctate dots present at the apex of the petals and along the margins; staminal column 1.5–2 cm. long, shorter than the petals, sharply 5-toothed at the apex; ovary lepidote-stellate, 5-celled, ovules 4 or 5 at the base of each

locule; capsule depressed-globose, 3–4.5 cm. diameter, 1.5–2 cm. high, leathery, indehiscent, fruiting calyx repand, often strongly undulate, 2 cm. in diameter; seeds usually 3 in each locule, obovoid, compressed and flattened on 2 surfaces, densely tomentose-stellate, often long-bearded at the base, secondary crispose pubescence often developed.

Common tree in coastal woods and edges of mangrove swamps or along sea coast on sandy soil. Widely planted in the tropics as a shade or ornamental tree. Flowers commonly eaten as food. Fruit used medicinally for treatment of skin eruptions.

BERMUDA: Holly Lodge, *Brown & Britton 1611* (NY, US), cultivated. BAHAMAS: New Providence; Hog Island, *Wilson 8321* (NY) in sterile condition in June; *Britton & Millspaugh 2176*, in sterile condition in Jan.; Nassau, *Curtis 173* (G, NY, US); Grantstown, *Wilson 8221*, (NY); Inagua, Mathew town, *Nash & Taylor 1473* (NY), cultivated; Turks Islands: Grand Turk, *Nash & Taylor 3840* (NY). CUBA: Havana: Playa del Rincon de Guanabo *Leon, Sanchez & Cubas 8493* (NY); Playa de Baracoa, *Leon 8422* (NY); Las Villas: Calicita, *Combs 522* (G, NY, US); Bahia de Cochinos, *Roig & Cremata 2167* (US); Punta Diablo, Cienfuegos Bay, *Britton & Wilson 6043* (NY); Soledad, *Howard 4176* (G), *Jack 4056* (US), *5347* (US), cultivated. Matanzas, Valley of the Yumuni, *Britton, Britton & Shafer 211* (NY); Oriente: Santiago, *Pastor 1811* (NY); Santiago Bay, *Sedro & Leon 3951* (NY); Gibara, *Shafer 1511* (NY, US); Santiago, *Underwood & Earle 1660* (NY); Las Minas, P. Principe, *Wright 1576* (G). JAMAICA: Bowden, *Britton 4017* (NY); Folly Point, *Fredholm 3166* (NY, US); Kingston, *Brown 356* (NY, US); Montego Bay, *Maxon & Killip 1623* (G); Rockport, *Killip 23* (US); Mandeville, *Miller 1406* (US); Hunts Bay, *Maxon & Killip, 326* (US). HAITI: Tortue Island, Basse Terre, *Leonard & Leonard 13919*, (G, NY, US); La Vallee, *Leonard & Leonard 15350*, (NY, US); Miragoane near Carenage, *Ekman 8578* (US); Miragoane, *Eyerdam 166* (G, US); Port-au-Prince, *Holdridge 1228* (NY, US). PUERTO RICO: Coamo, *Goll, Cook & Collins 751* (NY); Ponce, *Underwood & Griggs, 729* (NY, US); Fajando, *Heller 818* (US, NY), *Sintenis 1135* (US), *Evermann 1238* (US), *1246* (US); Parguera, *Sargent 452* (US); Vieques Island, Isabel Segunda, *Shafer 2392* (NY, US). ST. THOMAS: *Eggers 389* (G). ST. CROIX: Golden Rock, *Ricksecker 197* (NY, US); *Thompson 1056* (G); *Britton & Cowell 23* (NY). GUADELOUPE: *St. Rose 2779* (NY, US); Vieux-Fort, *Stehle 101* (NY). MARTINIQUE: Galian, *Duss 2024* (NY). ST. BARTS: Gustavia, *Questel, 128* (NY). ANTIGUA: St. Georges, *Box 1040* (US). MONTSERRAT: Plymouth, *Shafer 101* (NY, US). DOMINICA: Prince Rupert Bay, *Hodge 544* (NY, US); Pointe Ronde, *Hodge 2693* (G). GRENADA: Grand Anse, *Broadway S.N.* (NY, US); St. Georges, *Broadway S.N.* (NY, US). GRENADINES: Becquia, *Joseph B-160* (NY). TOBAGO: The Bay at Scarborough, *Broadway 4383* (G, US).

The specimens cited above were collected in flower or fruit in every month but June.

Specimens have also been examined from Florida, Panama, British Honduras, Colombia, Venezuela, British Guiana, Brazil, and Australia.

Local names: Cork-tree, Spanish Cork, Emajaguilla, Palo de Jaqueca, Santa Maria, Bendy-tree, Otaheite, Clamor (Puerto Rico); Álama Hiquillo, Majagua de la florida (Cuba); Gros Mahaut (Haiti); Álamo, Álamo blanco (Dominican Republic); Catappa (Guadeloupe); Seaside Mahoe (Florida).

ULBRICHIA Urb. Dansk. Bot. Arkiv. **4**: 7–8. 1924.

Armouria Lewton, Jour. Wash. Acad. **23**: 63–64. 1933.

Shrubs or trees, leaves alternate, petiolate, strongly angular-lobed, stipules linear, deciduous. Flowers solitary, axillary, on simple peduncles. Involucre of 3 linear to linear-lanceolate bracteoles, persistent or deciduous.

Calyx cyathiform, truncate to minutely 5-toothed, substipitate at the base. Petals 5, united at the base. Staminal column shorter than the corolla, 5-toothed at the apex. Ovary sessile, 5-celled, ovules 4–5 in each locule; stigmas and styles united. Capsule conical to ovoid, loculicidally 5-valved at the apex, densely lepidote-stellate-pubescent. Seeds obovoid, black, glabrous and shining, cotyledons black-dotted.

ULBRICHIA BEATENSIS Urb. Dansk. Bot. Ark. **4**: 8. 1924. *Armouria beata* Lewton, Jour. Wash. Acad. **23**: 64. 1933. *Thespesia beata* Hutchin. New Phytol. **46**: 136. 1947.

Shrub or tree to 8 m. tall; young branches lepidote-stellate; stipules linear, 5–6 mm. long; leaves orbicular in outline, the very young ones cordate-ovate, the older leaves 3–5-angled or lobed, 3–6 cm. long, 3.5–7 cm. broad, apex obtuse, base deeply cordate, the lobes overlapping, margin entire, lepidote-pubescent above, soft-lepidote-tomentose below, palmately 7–9-nerved, the midvein with a linear gland midway between base and apex; petioles 1–7 cm. long, peduncles 3–5 cm. long, slightly thickened below the calyx, bracteoles 3, linear-lanceolate, 3–4 mm. long, deflexed; calyx cyathiform 1.2 cm. long, 1.5 cm. diameter becoming 1.5 cm. long and 2.5 cm. diameter in fruit, densely and minutely lepidote outside, densely sericeous inside, truncate or minutely 5-toothed at the apex, constricted into a short stipe at the base; petals 5–6 cm. long, 3.5 cm. broad, cream-colored or white, black-dotted and lined in the middle, wooly-tomentose outside when young, glabrous inside; staminal column 3.5 cm. long, shorter than the petals, with 5 linear-lanceolate teeth at the apex; filaments 2.3 mm. long; ovary 5-celled, ovules 1.3–1.5 mm. long, densely lepidote-stellate-pubescent, capsule short-globose, 1.5–2 cm. long, 1.8–2.3 cm. diameter, apex abruptly and narrowly acuminate, the acumen 5 mm. long, densely lepidote-stellate pubescent, half enclosed in the calyx, loculicidally 5-valved at the apex; seeds obovoid, 7.5–11 mm. long, 5 mm. broad, 4.5 mm. thick, black, cotyledons black-resinous-dotted.

DOMINICAN REPUBLIC: Island of Beata, northern end, *Ostenfeld 312* (type not seen), flower in Feb.; rocky cliff near middle of west side of island, *Fairchild and Dorsett 2617* (US 1, 555, 481, TYPE of *Armouria beata*, duplicates and photographs), in flower and fruit in Jan. FLORIDA: U.S.D.A. Plant Introduction Garden, Coral Gables, *Loomis* s.n. (NY-sterile).

Illustration: Dansk. Bot. Ark. **4**: *pl. 1.* 1924.

The publication by Urban of *Ulbrichia* in a relatively obscure Danish publication has caused the genus to be overlooked by all recent students of the Malvaceae. *Ulbrichia beatensis* Urb. antedates *Armouria beata* Lewton and must replace the latter name. Both specimens were collected from Beata Island off the southern coast of the Barahona peninsula of the Dominican Republic.

Mr. Harold Loomis, director of the Plant Introduction Garden of the U. S. Dept. of Agriculture at Coconut Grove, Florida, was one of the botanists on the Fairchild-Dorsett expedition which found the plant described as *Armouria*. Mr. Loomis recognized the horticultural possibilities of this plant and brought back seeds from the type plant which have been grown at the Plant Introduction Garden. It was my pleasure to see the progeny of the type plant in flower at Coconut Grove in June of this year. The

handsome flowers are cream-colored and 4–5 inches in diameter. Unfortunately this tree has not set viable seeds. In discussing this collection Mr. Loomis told me only one group of these plants was found on Beata Island and it seems probable that the specimen described by Urban was taken earlier from the same plant as the Fairchild-Dorsett specimen.

A request has been made to the Bureau of Plant Industry that specimens be made of this interesting plant and that they be distributed to the various herbaria of the world. In the U. S. National Herbarium there are three sheets of photographs taken by Mr. Loomis of flowers and fruits of the specimen growing at Coconut Grove.

Atkinsia Howard, gen. nov.

Floris in spicis terminalibus aphyllis, calyce lignoso, persistenti, staminum columna corollam excedenti, capsula indehiscenti, seminibus glabris.

Trees. Branches and leaves densely covered with a lepidote or lepidote-stellate pubescence at least when young. Leaves alternate, petiolate; stipules not seen. Flowers solitary on stout peduncles in terminal leafless short spikes, flowering spikes with minute terminal buds often developing next year's growth. Involucre of 3 linear-lanceolate bracteoles, deciduous or persistent becoming contorted, falcate and woody in fruit. Calyx persistent, campanulate, truncate at the apex with 5 linear teeth, or variously lobed. Petals 5, imbricate, densely lepidote-stellate outside at the base, lepidote-scurfy outside above, glabrous inside. Staminal column longer than the corolla, filaments fused in pairs, anthers divaricate, strongly hippocrateriform. Styles united, stigmas clavate. Ovary lepidote-pubescent, 5 (3)-celled. Capsule indehiscent, globose, apiculate, 1–3-celled with remnants of the others; seeds 1–3 in each cell, black, glabrous; cotyledons folded, black-punctate. Fruiting calyx woody, irregularly split, investing the fruit.

TYPE SPECIES: *Maga cubensis* Brit. & Wils.

Atkinsia cubensis (Brit. & Wils.) Howard, comb. nov. (figs. 7–14). *Maga cubensis* Brit. & Wils. Mem. Torrey Club **16**: 81. 1920. *Montezuma cubensis* Urb. Repert Sp. Nov. **18**: 117. 1922. *Thespesia cubensis* Hutchin. New Phytol. **46**: 135. 1947.

Tree to 17 m. tall; branches stout, densely lepidote-pubescent, lenticels round, conspicuous; leaves ovate-orbicular to ovate-cordate, 6–10 cm. long, 7–13 cm. broad, apex acute or acuminate, base deeply cordate or rarely subtruncate, coriaceous, margin entire, densely lepidote-stellate on both surfaces becoming glabrate, palmately 5–7-nerved at the base, midvein with linear gland about the middle of its length, the nerves connected at the base on lower surface by a membranaceous web forming domatia for scale insects; petioles 4–7.5 (10) cm. long; stipules not seen; flowers solitary on stout peduncles 2–6 cm. long, 5–7 clustered on leafless terminal shortened shoots; bracteoles 3, linear-lanceolate, 7–9 mm. long, caducous or persistent becoming woody and contorted; calyx campanulate, 9–12 mm. long, 1–1.7 cm. diameter, truncate with linear-subulate teeth to 3 mm. long or variously ruptured by the expanding bud, densely lepidote-stellate outside, densely lepidote-stellate or tomentose inside; petals 5, 3 cm. long, 1.3–1.5 cm. broad, yellow-white to yellow-brown becoming darker with age, black dots arranged in rows along the veins; staminal column 5–6 cm. long, twice as long as the corolla, filaments usually fused in pairs, 2 mm. long; ovary 3–5-celled, ovules 1–3 in each

FIGS. 7–14. *Atkinsia cubensis* (*Jack 4959*). FIG. 7. Habit showing leafless cluster of flowers and persistent woody calyx. Pubescence omitted. FIG. 8. Bud. FIG. 9. Cross section of fruit with two fertile locules. FIG. 10. Cross section of seed showing black punctate cotyledons. FIG. 11. Longitudinal section of seed. FIG. 12. Side view of seed. FIG. 13. Lower surface of leaf blade showing axillary webs and scale insect domatia. FIG. 14. Flower showing staminal column exceeding the corolla. All drawings × ½.

locule; capsule depressed-globular, apiculate, 2.5 cm. long, 3 cm. diameter, fleshy, becoming woody, the inner portion of the wall heavily filled with black resinous material, surface sparsely lepidote; seeds obovoid or rounded, flattened on 1–2 sides, 8–13 mm. long, 7–8 mm. broad, 4.5–7 mm. thick, glabrous.

CUBA: Las Villas: Caunao River, *Jack 4959* (NY, US), *Jack 5010* (NY, US), in flower and fruit March; Caunao River at Iguana Point, *Jack 5132* (NY, US), in fruit in April; Guabiro, near Soledad, *Jack 6955* (US), in flower in March; Cienfuegos Bay, Punta Diablo, *Britton & Wilson 6045* (NY, Type and two isotypes), in flower in March; Rincon to Banao, *Shafer 12175* (NY, US), in flower in Feb., *Shafer 12311* (NY), in fruit in March. Camaguey: La Gloria to Pilota, *Shafer 566* (G, NY), sterile in Feb. Oriente: Papayo of the Sevilla tract, Mandingo hill, *Ekman 9444* (NY), at 700 m. alt., sterile in Aug.; San German, *Ekman 6355* (NY), sterile in Aug.; Rio Cauto at Central Cauto, *Ekman 16124* (NY, US), in flower in Jan.

Urban (Repert. Sp. Nov. **24**: 237. 1928) also cites two Ekman collections from Pinar del Rio which I have not seen, *Ekman 17667* collected between Chambergo and Charco del Toro, and *Ekman 12867*, collected near Mariel and Tinaya.

Local names: Negra cuba, Majagua de Cuba (fide Ekman), Majagua peluda (fide Urban), Majagua negra (fide Leon).

The original description of *Atkinsia cubensis* by Britton and Wilson, under the generic name of *Maga*, is sketchy. Urban elaborated and corrected this description citing additional material collected by Ekman (Repert. Sp. Nov. **24**: 237. 1928).

Britton and Wilson described the calyx as circumscissile. I have examined the type and two isotype specimens as well as the additional material cited above and find the report of this character to be entirely an error. The fruiting calyx of *Atkinsia cubensis* is woody and enlarged but still encloses the depressed capsular fruit (fig. 7). During the enlargement the fruiting calyx is ruptured and the sections are irregular. They persist on the fruiting peduncle after the capsule falls (fig. 7). The fruiting peduncles finally break free from the branch or the main axis with the calyx still intact. It was on the supposedly circumscissile calyx that Britton and Wilson assigned this species to *Maga* Urb., and Hutchinson still uses this erroneous character to separate this species in his treatment of *Thespesia*.

The nerves of the cordate leaf are stout and palmately arranged in *A. cubensis*. On the lower leaf surface the nerves are joined at the base by a membranaceous web forming small cavities. In many cases these cavities are filled with scale insects and might properly be called domatia. Whether or not the insects are present, the membranaceous webs are always present and characterize this genus and species. The webs frequently extend to a point between the nerves and often show signs of a strong vascular ridge or fold extending into the web and into the point.

Hutchinson describes the leaves of *A. cubensis* as being "very deeply cordate or auriculate, the auricles often overlapping." Such a condition does not exist in the material I have seen. The leaf base is slightly cordate and the auricles never overlap.

The inflorescence is described by Hutchinson as sympodial. Actually 5–7 flowers may be produced at the apex of a stout branch. In flowering condition this axis is without leaves but very young leaves have been observed in

some specimens after the fruits have fallen. The following year's growth is often produced through a terminal bud on this floral axis. Older specimens of several years' growth will show this region of flower production appearing almost as a short shoot condition.

The ovary is 5-celled in most of the flowers I have examined. In fruit, however, usually only 3–4 locules will be fully developed with plump seeds.

The genus *Atkinsia* is named in honor of the Atkins family, especially Katherine Atkins and the late Edwin Atkins, who have done so much for the study of botany and of tropical botanical problems through the establishment of the Atkins Garden and Research Laboratory of Harvard University at Soledad, near Cienfuegos, Cuba.

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THE MORPHOLOGY OF CHLAMYDOMONAS CHLAMYDOGAMA, SP. NOV.

HAROLD C. BOLD

During the past three years while engaged in studying clonal cultures of *Chlamydomonas* from soil samples, with the ultimate purpose of obtaining data for comparsion with those obtained by Moewus (1938a,b, 1939a,b,c, 1940a,b,c, 1943), the writer isolated an interesting form from a Venezuelan soil sample.[1] The ease with which the organism can be maintained in culture, as well as its readily demonstrable sexuality impel the writer to describe its morphology, and to make it available for demonstration and further study by others.

As noted by Smith (1946) in his brief summary of some aspects of Moewus' work, the certain identification of species of *Chlamydomonas* and related organisms is fraught with difficulties. Many specific descriptions are markedly incomplete, unsupported by prolonged critical observations, cultural studies, and adequate illustrations. Furthermore, the herbarium specimens available usually do not reveal the morphological details on the basis of which species are distinguished. Finally, the nature of the zygospore and its behavior upon germination have been recorded for relatively few species.

The present organism (figs. 1–21) belongs obviously in the subgenus *Agloë* (Pascher 1927, Gerloff 1940) of the genus *Chlamydomonas*, and is in some respects most similar to *C. sylvicola*, a form incompletely described by *Chodat* (1921). Although a number of species of *Chlamydomonas* possess walled gametes, this feature is so marked and readily observable in the present organism that the latter will be described as:

Chlamydomonas chlamydogama Bold, sp. nov. Cellulae e 13.2 ad 26.4 μ longitudine, e 5.0 ad 9.0 μ latitudine, ellipsoidales vel cylindroidales, saepe quommodo reniformes. Muri cellulares frequenter separati ab protoplastis in parte posteriore. Cellulae sine papilla; vacuoles contractiles gemini, anteriores. Stigma instans, in parte anteriore. Chromatophora velut H, cum pyrenoide unico axiale. Nucleus posterior. Propagatio asexualis per 2 vel 4 cellulas intra cellulae maternae membranum ortas. Propagatio sexualis heterothallica et isogamica; zygotes non rubri, semper virides, cum membranis unornatis, quadrifariam germinantes. Hab.: In solum Venezuelensem.

[1] The writer is indebted to Dr. Kenneth B. Raper, Northern Regional Research Laboratory, U.S.D.A., for making foreign soil samples available.

Material and Methods. Air dry soil of sample W-16 (from Venezuela) was introduced into Erlenmeyer flasks containing 100 ml. of modified sterile Bristol's solution (Bold 1942). The solution is prepared as follows: six stock solutions, 400 ml. in volume are employed, each containing one of the following salts in the concentration listed:

$NaNO_3$	10.0 grams	KH_2PO_4	7.0 grams
$CaCl_2$	1.0 gram	$MgSO_4$	3.0 grams
K_2HPO_4	3.0 grams	NaCl	1.0 gram

10 ml. of each stock solution are added to 940.0 ml. of Pyrex-distilled water. To this are also added one drop of a 1.0 per cent $FeCl_3$ solution and 2 ml. of minor elements solution (Craig & Trelease 1937).

The cultures were illuminated in an artificial cooled light (Bold 1936) or by fluorescent light of approximately 50 foot-candles intensity. Within two weeks after setting up the cultures a delicate, green, positively phototactic ring of motile algae appeared in the flasks, from which individual *Chlamydomonas* cells were isolated with micropipettes. The organisms may be maintained also in Knop's solution as prepared by Moewus (1940b), and on solid media in which either Bristol's or Knop's solutions have been compounded with 1.5 per cent agar. The cells are nonmotile on agar, but remain motile in liquid cultures with adequate nutriment and illumination. Microscopic study over prolonged periods was most successful in hanging-drop preparations.

Observations. The specific description given previously is based on several years' observation of clonal cultures isolated from soil. The variations in cell size probably represent cells in various stages of development after their liberation from parent cells at the conclusion of cell division. The cell wall lacks a papilla, but two small flagellar orifices are apparent (fig. 18) when the protoplast contracts during cell division. Mature cells frequently have their protoplasts markedly withdrawn from the posterior portion of the wall (figs. 2, 4, 5). Study of cells stained with methylene blue indicates that this contraction is not induced by a thickening of the basal portion of the wall, but rather that an autonomous withdrawal of the protoplast occurs. The latter may also be slightly withdrawn from the anterior portion of the wall (figs. 1, 2, 4, 5), and in some cases forms a papilla-like beak (fig. 5). The flagella are approximately of body length.

Although somewhat variable, the chloroplastid in median, longitudinal, optical section (figs. 1, 2) exhibits the "H"-shaped structure characteristic of members of the subgenus *Agloë*. The posterior and anterior openings are frequently small, with the prominent single pyrenoid lying in the central bridge of the chloroplastid. Two contractile vacuoles, which function alternately, occupy the anterior portion of the protoplast (figs. 1, 2, 5), and, as

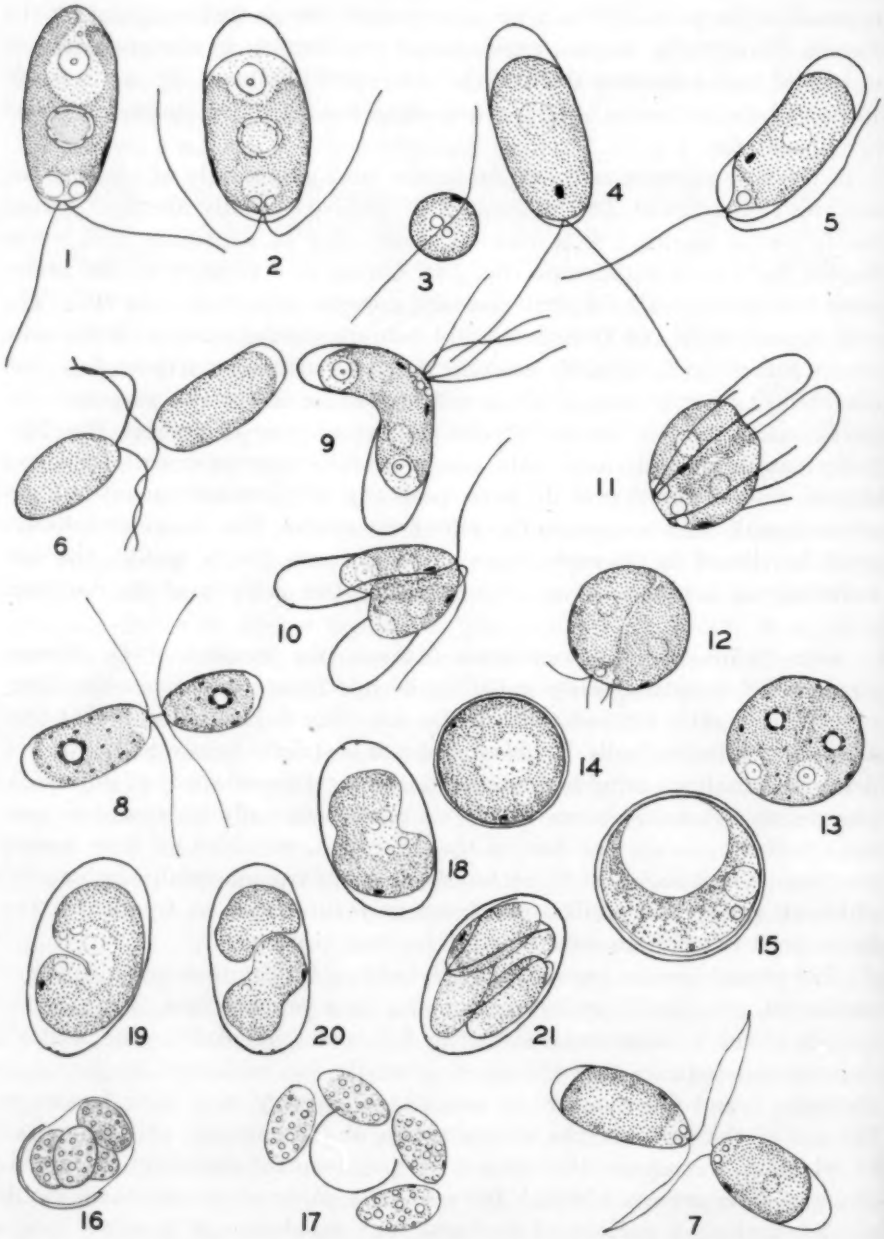
is usual in the genus, lie in a plane perpendicular to that occupied by the flagella (fig. 3). The stigma, which varies considerably in size and form, is embedded in the anterior third of the chloroplastid (figs. 1–5). As in many species of the subgenus *Agloë*, the nucleus lies in the posterior, colorless cytoplasm (figs. 1, 2, 9).

In thriving cultures cell division occurs most abundantly at night if the cultures are darkened. The products of division are usually liberated during the following morning. Cell division occurs only in nonmotile cells whose flagella have been withdrawn (fig. 18). Owing to a rotation of the protoplast within the wall the first cleavage appears transverse (fig. 19). The cells figured as 18 and 19 indicate that a duplication of contractile vacuoles occurs before cytokinesis. No evidence for their origin by division has been observed. As a rule each dividing cell undergoes one or two successive bipartitions so that the daughter cells are two or four in number (fig. 21). Immediately after division only one of the division products contains a stigma, presumably that of the parent cell (fig. 21), but subsequent to liberation a small stigma appears in each of the others. The daughter cells become flagellated in the early morning and become feebly motile; the surrounding mother wall is ruptured by the violent activity of the daughter cells.

Like *Chlamydomonas eugametos* Moewus, the gametes of *C. chlamydogama are* morphologically indistinguishable from vegetative cells. However, their slightly but constant smaller size (figs. 6–11) indicates that they are recently divided cells. *C. chlamydogama* is strictly heterothallic, no evidence of sexuality having been observed in several years' study of individual (segregated) clonal cultures. Of the six clones originally isolated, two were apparently of one sex and four of the other, as determined by their mating reactions. The gametes of *C. chlamydogama* are fundamentally isogamous; although gametes of unlike size frequently fuse, just as frequently two large and two small gametes may be observed uniting.

The sexual process occurs regularly when cells from clonal cultures of unlike sex are mixed together in hanging-drop preparations, in which the details of the process may be readily followed (figs. 6–15). The writer's observations indicate that the speed, intensity (as evidenced by degree of clumping), and duration of the sexual process vary with such factors as the age of the cultures, the concentration of the gametes, and others, all of which will comprise the subject of a subsequent contribution. Unlike Moewus' *C. eugametos* (1938a), the cells of *C. chlamydogama* remain motile during prolonged periods of darkness, but copulation of gametes occurs only in illuminated cultures.

The sexual process from the time the gametes first approach (fig. 6) until the complete withdrawal of the flagella by the zygote (fig. 13) occupies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between 1½ and 2 hours. If hanging-drop preparations are examined immediately after the clones are mixed, a rather marked decrease in motility is apparent, but within five minutes active motility recurs. Certain of the cells become anchored to the coverglass by their flagellar extremities, and exhibit rather violent, jerky movements. Others, which have been free-swimming, aggregate around the nonambulatory cells forming more or less extensive groups in which individual pairs are formed, at first by entanglement of flagella (fig. 6), but almost immediately the flagella appear to agglutinate at their tips (fig. 7). Such pairs move by jerky movements, and never far from the point of original union, apparently because the flagellar tips are rather firmly attached to the substratum. No evidence for negative phototactic reactions of fusing gametes is apparent in hanging-drop cultures. The cells continue in this condition (fig. 7) often for more than an hour, undergoing violent but localized movements during which the anterior poles of the cells are vigorously brought together. The rupture of the cell wall of each gamete is achieved probably through both mechanical and chemical means. Evidence of the latter is available in the examination of cast-off gamete walls which usually have a frayed, hydrolyzed appearance at their anterior portion.

The first permanent union of the protoplasts occurs in the region of their blepharoplasts, and at the moment of union, the flagella, which have been actively motile while still terminally united, separate entirely from each other (fig. 8), and subsequently carry on only very feeble motion. Careful observation indicates that frequently at this stage the mating gametes are connected by a protoplasmic thread (fig. 8), also observed by

Explanation of figures 1–21

All figures were drawn with the aid of a Leitz camera lucida, and reduced ½ in reproduction. The approximate magnification is 1553, except figures 16, 17, for which it is 700. All are from living material except where indicated in the legends.

FIG. 1. Vegetative cell in median longitudinal optical section (m.l.o.s.); protoplast in contact with posterior portion of wall. FIG. 2. Vegetative cell in m.l.o.s., protoplast contracted posteriorly. FIG. 3. Anterior polar view of vegetative cell. FIG. 4. Vegetative cell in surface view. FIG. 5. Slightly reniform type of vegetative cell, protoplast beak-like anteriorly. FIGS. 6–15. Sexual reproduction. FIG. 6. Initial entanglement of flagella. FIG. 7. Terminal agglutination of flagella. FIG. 8. Gametes stained with IKI solution, protoplasmic thread apparent between blepharoplasts. FIG. 9. Early stage in protoplast fusion. FIG. 10. Gamete protoplasts escaping from walls. FIG. 11. Later stage, gamete protoplasts almost entirely shed. FIG. 12. Still later stage, gamete protoplasts still delimited, flagella disappearing. FIG. 13. Zygote stained with IKI solution. FIG. 14. Zygospore with wall, 48 hours after union, one pyrenoid is markedly smaller, stigmata still visible. FIG. 15. Zygospore 1 week after union of gametes; large vacuole-like and smaller oil droplets visible. FIG. 16. Germination of the zygospore on Bristol's agar medium. FIG. 17. Liberation of products of zygospore germination on Bristol's agar. FIGS. 18–21. Asexual reproduction, cell division. FIG. 18. Rotation and first cleavage of protoplast; note duplication of contractile vacuoles, but not stigma. FIG. 19. Stage similar to 18, but cleavage unilateral. FIG. 20. Early stage in second cleavage. FIG. 21. Four daughter cells, flagellated, just before liberation.

Strehlow (1929) in *Polytoma uvella*. Once their contact has become established, union of the gamete protoplasts (figs. 9–13) proceeds with great rapidity: they flow out of the cell walls, and fuse completely leaving the empty gamete walls behind. The flagella become shortened and attenuated, and finally disappear (fig. 13). Observation of living cells indicates that they are withdrawn, although it is possible that this appearance is due to acropetal hydrolysis. The individual gamete protoplasts are recognizable within the zygote often for as long as 24 hours after fusion, as are also their contractile vacuoles, pyrenoids, and stigmata. The exact time of nuclear fusion has not yet been determined. After 48 hours, however, the individual gamete protoplasts are no longer recognizable, a wall is secreted around the zygote (fig. 14), and one of the gamete pyrenoids ultimately disappears. The zygospore then enlarges considerably (fig. 15), and, if retained in the same culture medium in which fusion occurred, loses some of its chlorophyll and develops droplets of colorless oil.

Zygospore germination has been obtained by transferring zygospores a week after their formation from the hanging-drop preparations to the surface of nutrient agar. The first germinations occurred within 48 hours. In every case observed the contents of the zygospore underwent two successive bipartitions resulting in the liberation of four daughter protoplasts (figs. 16, 17). These became motile when flooded with liquid nutrient solution.

Discussion. In spite of implied criticism (Philip & Haldane 1939) of Moewus' numerous contributions dealing with sexuality in *Chlamydomonas* and other organisms, one can not avoid being impressed and stimulated by the importance of the fundamental problems they involve. Smith (1946) has expressed a similar view, and has reviewed some of the more important aspects of Moewus' work, which have no direct bearing here. A complete and final confirmation of Moewus' results can be effected only by using precisely the same organisms which the latter studied, but significant comparative data will certainly be obtained by studies of sexuality in other species.

The observations reported in this paper are preliminary in that they are entirely morphological; further work on other aspects is in progress. However, although sexual union in *Chlamydomonas* species has been reported again and again, the more detailed phases of the process have often been omitted. The ease with which *C. chlamydogama* may be cultivated as well as its ready manifestation of sexuality suggest to the writer that it should be made available both for instructional and research purposes.[2]

[2] Unialgal cultures of the heterothallic strains W16–1 and W16–2 of *C. chlamydogama* will be sent at the request of anyone desiring them for purposes of teaching and research. The cultures are maintained in the modified Bristol's solution described in the text. It is regretted that it will be necessary to request a fee of one dollar to cover costs of mailing and maintenance of cultures by a laboratory technician.

From a morphological viewpoint several of the observations reported herein are of interest. One is inclined to infer that those gametes which first become attached by their flagella to the substratum, and which subsequently unite with more actively motile individuals, are female. There is some similarity here with Hartmann's (1934) description of sexuality in *Ectocarpus siliculosus*. More convincing proof of the female nature of the less active gametes of *C. chlamydogama* would be their regular preference for the male gametes of a heterogamous species.

Although many accounts of gamete union in the algae emphasize the importance of flagellar entanglement in effecting fusion, it certainly plays a minor role in *C. chlamydogama;* the entanglement here is only momentary, and is followed immediately by what appears as a terminal agglutination effected chemically. This condition persists for an hour or more, and the evidence indicates that during this period dissolution of the gamete walls is achieved both mechanically and by the mutual secretion of some hydrolysing agent. Experimental evidence for the chemotactic nature of gamete union has been reported by Moewus (1939b). The union of the gamete protoplasts themselves is fundamentally similar to the same process in Zygnematalean genera like *Closterium*.

SUMMARY

1. A specific diagnosis of an undescribed species of *Chlamydomonas, C. chlamydogama,* is presented.

2. The organism was originally isolated from a soil sample from Venezuela, and clonal cultures may be readily maintained in Bristol's, Knop's, and probably other media.

3. The morphology of the organism is described and illustrated.

4. *C. chlamydogama* is strictly heterothallic; sexuality is readily manifested when organisms from clonal cultures of different sex are brought together in hanging-drop preparations.

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VARIATION IN A NATURAL POPULATION OF PLANTAGO ARISTATA

RICHARD H. GOODWIN

The extreme variability of the little plantain, *Plantago aristata* Michx., first atttracted my attenion while I was making a survey of the flora of Mendon Ponds Park, Monroe County, New York (Goodwin 1943). This species was found growing in profusion in and beside a bridle path which runs along the sandy crest of an esker. Collections were made in 1941 and 1942 at this station.

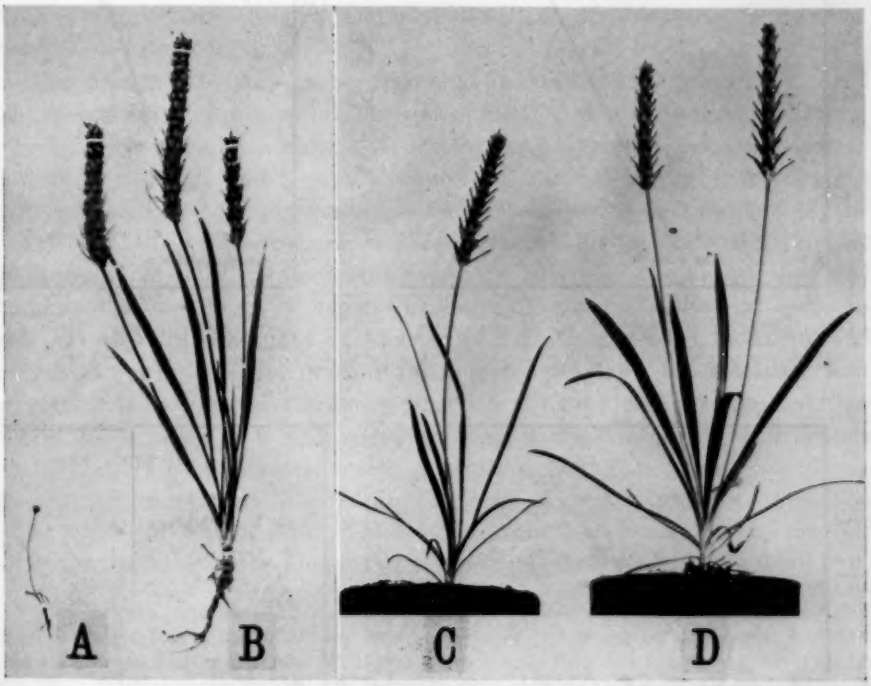


FIG. 1. Photographs of *P. aristata*. × ⅓. A. Depauperate, one-flowered specimen from Mendon. B. Large, vigorous specimen from Mendon. C, D. Plants grown in greenhouse from seeds of specimens similar to those shown in figures 1A and 1B, respectively.

P. aristata is a midsummer-flowering annual with a basal rosette of linear leaves and one or more flowering scapes. The smallest plants collected had solitary, one-flowered scapes about 3 cm. long and two thread-like leaves about 1.5 cm. long (figure 1A); the largest had as many as seven scapes over 20 cm. long with up to 76 flowers per scape and with as many as 13 leaves

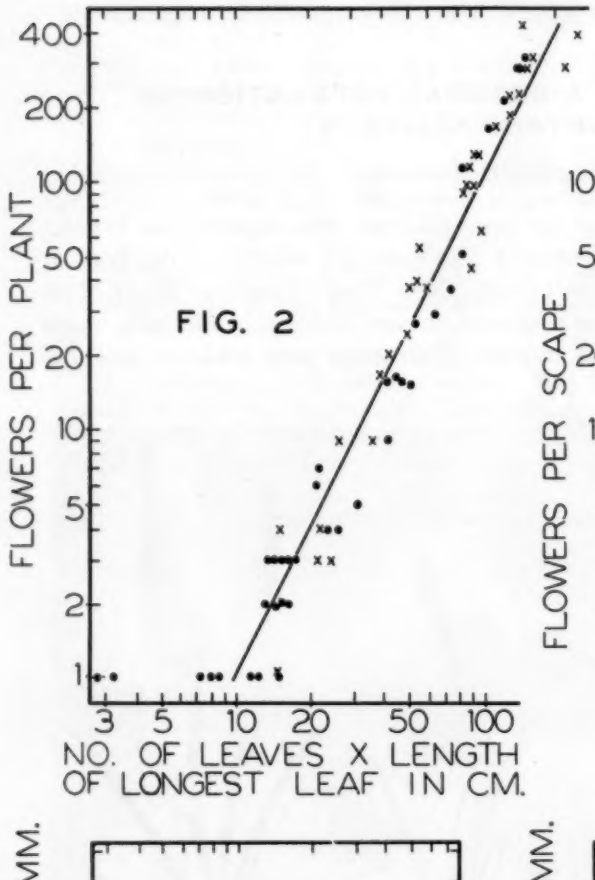
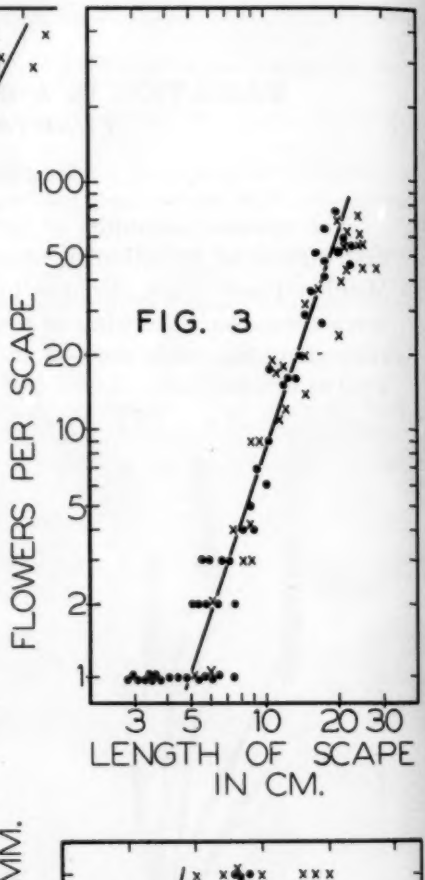


FIG. 2



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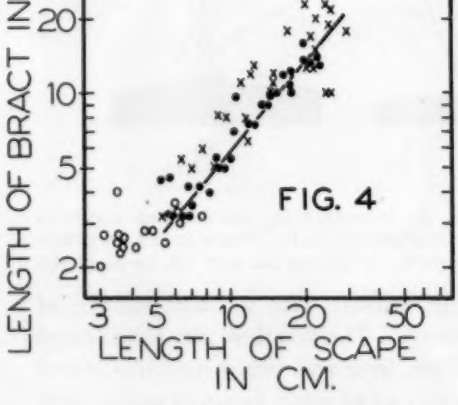

FIG. 4

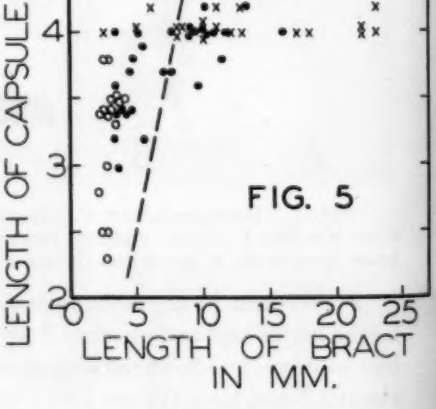

FIG. 5

up to 13 cm. in length. A large plant is shown in figure 1B. All plants collected had reached maturity; that is, the capsule contained mature seeds. Some of the largest plants still had some immature flowering scapes, but only the fully-developed ones were measured. The following measurements were made; number of leaves and length of the longest leaf; number and length of the scapes; number of flowers per scape; length of the capsule (from the base to the point of reflection of the corolla lobes); length of the seed; and length of the lowest bract of the inflorescence.

Similar data were also obtained from the following specimens from New York in the Cornell University Herbarium: Flushing, Long Island, July 15, 1936, *J. Monachino 93;* Islip, Suffolk County, Long Island, June 24, 1925, *W. C. Muenscher 16291;* Lake Ronkonkoma, Long Island, August 17, 1938, *Muenscher & Curtis 6497;* Waneta Lake, Schuyler County, July 11, 1934, *R. T. Clausen 1389;* Ithaca, August 1, 1904, *E. M. Cipperly,* September, 1903, *F. W. Foxworthy.*

The first relationship to be presented is one between vegetative vigor and the extent of reproduction. If we assume that there is a direct relationship between these two phases of development, then the total number of flowers per plant, which is a measure of the amount of reproductive material produced, might be expected to increase as a function of the quantity of the photosynthetic tissue; however, in this study the product of the number of leaves per plant times the length of the longest leaf has been used as an index of vegetative vigor. Figure 2 shows the relationship between total number of flowers and the leaf length index plotted on a double logarithmic grid. With the exception of the smallest, one-flowered plants, all the plants measured fall nicely along a straight line which has a slope of 2 and which satisfies the mathematical expression: $y = bx^2$, where b is a constant with a value of 10^{-4}. This shows that reproduction in these plants is a definite function of their vegetative vigor. The exact significance of the value x^2 is not certain, but it may not be too bad an approximation of the amount of photosynthetic tissue. If this were true,

FIG. 2. Total number of flowers per plant (y) plotted on a double logarithmic grid against the product of the number of leaves per plant and length of the longest leaf (x). The line represents the formula $y = 10^{-4}x^2$. It is a close, but not necessarily best, fit for the data. Dots: data for Mendon specimens. Crosses: data for other New York collections. FIG. 3. Number of flowers per scape (y) plotted against length of scape (x) on a double logarithmic grid. The line represente the expression $y = bx^3$, where b is a constant with a value 8×10^{-6}. This relation becomes a straight line with a slope of 3 when plotted logarithmically ($\log y = \log b + 3 \log x$). Symbols as in figure 2. FIG. 4. Length of lowest bract (x) plotted against length of scape (y) on a double logarithmic grid. Open circles: Mendon specimens with one flower only. Dots: Mendon specimens with two or more flowers. Crosses: data for other New York collections. FIG. 5. Length of capsule plotted against length of lowest bract. The ratio: length of bract/length of capsule, is less than 2 for all plots falling to the left of the broken line. Symbols as in figure 4.

their reproduction would appear to be directly proportional to their photosynthetic capacity.

Within the inflorescence, there is a close and direct relationship between the length of scape and the number of flowers produced thereon. Figure 3 shows the data plotted on a double logarithmic grid. With the exception of the smallest of the one-flowered plants, the plots fall along a straight line which has a slope of 3. The formula expressing this relationship is $y_o = bx_o^3$, where y_o equals the number of flowers, x_o equals the length of the scape in mm., and b is a constant. Since y_o essentially represents a volume, and x_o a linear dimension, raising x_o to the third power should make the two sets of measurements comparable.

The formula of heterogonic growth (Huxley 1932) is $y = bx^k$, where y is the size of a particular structure, x is the size of the whole organism, k is the ratio of the growth rate of y to the growth rate of x, and b is a constant. Applying this to the scape and inflorescence, $y = y_o$, $x = x_o^3$, $b = 8 \times 10^{-6}$, and $k = 1$. This value of k may be interpreted as indicating that inflorescence and scape have the same relative rates of growth.

The relation between length of scape (x) and length of the bract subtending the lowest flower (y) is shown in figure 4. Data for scapes with one flower only have been indicated by open circles, scapes with two or more flowers, by dots. There is a linear logarithmic relationship for the latter group of plots. Applying the formula for heterogonic growth, $y = bx^k$, $b = 0.023$, and $k = 1.2$, for the Mendon collections. This value of k means that the lowest bract grows faster, relatively, than the scape.

Data from specimens collected elsewhere in New York State (crosses) show significant deviations from the above relationship, suggesting hereditary differences in the value of b. A more exhaustive set of measurements from specimens collected over a still wider range would doubtless show still greater deviations. For specimens in the Cornell University Herbarium of the very similar species, *P. Purshii* R. & S., collected from Texas to California north to Michigan and Washington, the relationship between number of flowers and scape length was very distinct for the various geographical localities represented, b appearing to be the variable rather than k.

There is an interesting taxonomic consequence of the heterogony of the bracts of *P. aristata*, namely, that depauperate specimens have the lowermost bracts as short as, or shorter than, the flowers which they subtend, the flowers being nearly constant in size. The length of the bracts relative to that of the flowers has been used as a key character to distinguish *P. aristata* from other species within the genus. For example, in the species key in *Grays New Manual* (Fernald & Robinson 1908), plantains with "bracts much exceeding the calyx," and in the *Flora of Indiana* (Deam

1940), plantains with "lower bracts at least twice as long as the flowers" belong to this species rather than to *P. Purshii* or *P. lanceolata*. An examination of figure 5 shows that a fairly high proportion of the smaller plants of the Mendon population possess bracts much less than twice the length of the calyx (all plots falling to the left of the broken line). In this species capsule length is very nearly the same as that of the calyx. Data for collections from other New York localities have been included (crosses).

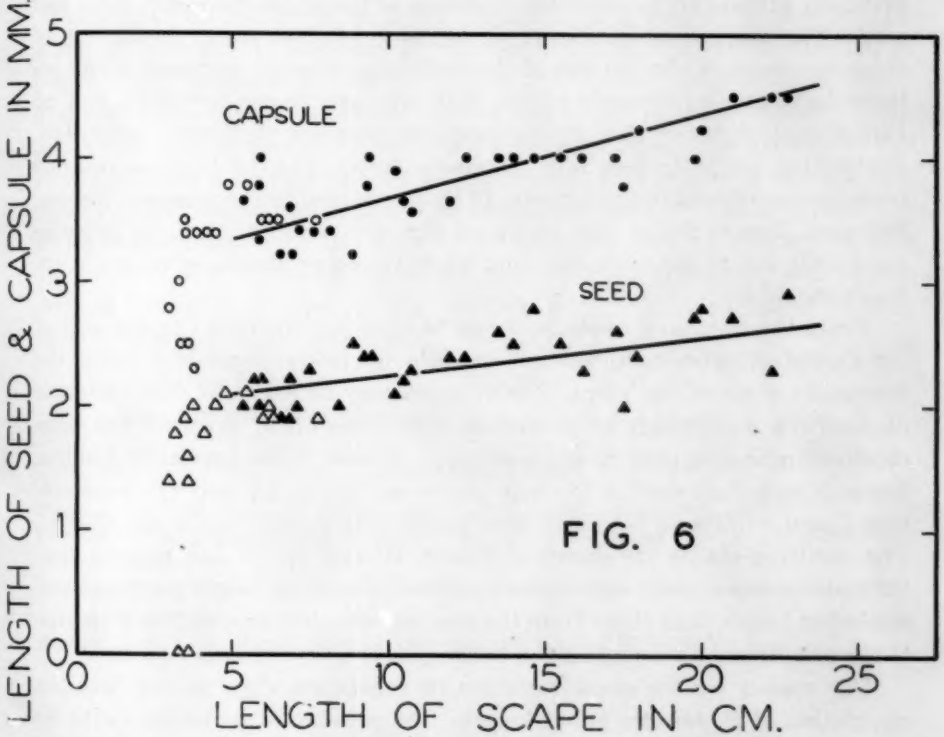

FIG. 6. Length of seed (triangles) and capsule (circles) plotted against length of scape. Open symbols: plants with one flower only; solid symbols: plants with two or more flowers.

Only three of these other collections contained depauperate plants with relatively short bracts. A collection containing only depauperate specimens will probably be a relatively rare occurrence and so may not be too important from the point of view of constructing a key. The taxonomist should bear in mind, however, that variation of this type may be controlled primarily by the size attained by the plant—that it is a dependent and not an independent variable.

The length of seed and capsule have been plotted against length of scape

in figure 6. For plants with more than one flower per scape, there is a definite increase in capsule length (about 30 per cent) and in seed length (about 25 per cent) with increase in length of scape. It should be recalled that length of scape is correlated with the vegetative vigor of the plant. For plants with only one flower per scape there is a rapid falling off of flower and seed size with additional decrease in scape length.

When the plant passes into the reproductive phase of development it evidently utilizes all its available resources in the production of flowers and seeds. The number of flowers produced is dependent upon the extent of these resources; while the size of the individual flowers increases only to a limited extent. Depauperate plants with only one flower, however, can no longer control flower size by varying the number of flowers produced. Everything available goes into the single flower and the two boat-shaped seeds contained within the capsule. If there are insufficient reserves for one full-sized flower, flower size and seed size are reduced; and, in extreme cases, only one of the seeds develops, while the other aborts, or no seeds are produced at all.

From the foregoing analysis, it can be seen that variation in the size of the reproductive structures of *P. aristata* is closely dependent upon the vegetative vigor of the plant. The question may be asked, is this variation in vigor due to heredity or to environment? One bit of evidence has been obtained indicating that variation in vigor, at least, is not primarily genetic. Seeds from plants similar to those shown in figures 1A and 1B were collected, and from them seedlings were grown side by side in the greenhouse. The resulting plants are shown in figures 1C and 1D. It can be seen that both plants are normal and vigorous. Plants from the larger parents were somewhat larger than those from the smaller ones, but this may well be due to the nutritional advantage given to the plants from the larger seeds.

The reason for the great variation in vegetative vigor in the Mendon population of *P. aristata* is not known. One possible explanation might be that in nature there is a difference in the time of germination of the seeds, which, in turn, might be due to a number of different causes, such as depth of the seed in the soil, overturning of the soil in the bridle path by horses' hooves, etc. The seedlings germinating early in the season would have a head start over those germinating later on. If flower induction were photoperiodically controlled in this species, then the size of the plant at the onset of flowering would determine the extent of the reserves available for flower production.

In order to check the above-mentioned hypothesis, seeds were planted in pots and germinated in the greenhouse at monthly intervals from January through April. Germination was somewhat sporadic. All the plants thus

grown flowered in May, regardless of the date of germination. This suggests that *P. aristata* is indeed a long-day plant. The size of the plants varied considerably, but no one-flowered specimens were obtained. The fact that flowering occurred earlier in the greenhouse than it does in nature is doubtless due to some of the many environmental differences between greenhouse and natural conditions.

SUMMARY

An analysis has been made of variation in a natural population of *Plantago aristata*. It has been shown that the reproductive capacity of a plant of this species is at least roughly proportional to its vegetative vigor, and that variations in number of flowers, and length of scape, capsule, seeds and bracts are all correlated with this vegetative vigor. The growth of the bracts exhibits a certain amount of heterogony. Differences in size are due chiefly to environmental and not to hereditary factors. The suggestion is made that variation in the time of germination may be responsible for variation in size of the plants at the time of floral initiation, and that a critical long-day photoperiod may initiate flowering in all plants of this species irrespective of their size.

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EMBRYONIC DIFFERENTIATION IN TAXUS CUSPIDATA[1]

CLARENCE STERLING

The development of organized meristems and the differentiation of tissues laid down by these meristems are subjects which have continually interested plant morphologists and physiologists. However, problems of polarity, meristematic structure, and organ differentiation are still far from being satisfactorily resolved. Although various approaches have been attempted, newer techniques are constantly being enlisted in an effort to investigate these questions. In the thought of contributing added data toward a better understanding, the present study considers the histogenetic aspects of meristematic development and tissue differentiation in the late embryo of *Taxus cuspidata*. This investigation is a continuation of the ontogenetic study of early embryogeny in the same species (Sterling 1948b).

Materials and Methods. The embryos used in this investigation were obtained from the same source described in the study of gametophyte development (Sterling 1948a), and the killing, fixing, and staining procedures are similar. However, it should be noted here that the Carnoy mixture often caused excessive shrinkage in the cytoplasm. Drawings were made by camera lucida, and photomicrographs were taken with a Leitz "Micam" attachment.

Initiation of Late Embryogeny. In the embryo which is becoming massive, growth activity is centered in a small group of initials at the surface of the free apex of that embryo. The initial cells are the progenitors of the other cells in the enlarging, undifferentiated apex. From these initials, all other cells of the embryo appear to diverge in periclinal rows. The anticlinal walls can be envisaged as concentric arcs radiating from the initial region, indicating the successive growth increments in apical development. Thus the free apex of the embryo is organized like the apical meristem of a shoot. At this stage of development, this meristem at the free apex is the only center of mitotic activity in the embryo. Usually, no further cleavage is to be found in the ontogeny of the *Taxus* embryo. However, occasional bilobed embryos have been found at this stage, as has also been reported in *Ginkgo* (Lyon 1904), *Torreya* (Buchholz 1940), and *Welwitschia* (Pearson 1910).

On superficial examination, there can be seen a clear demarcation be-

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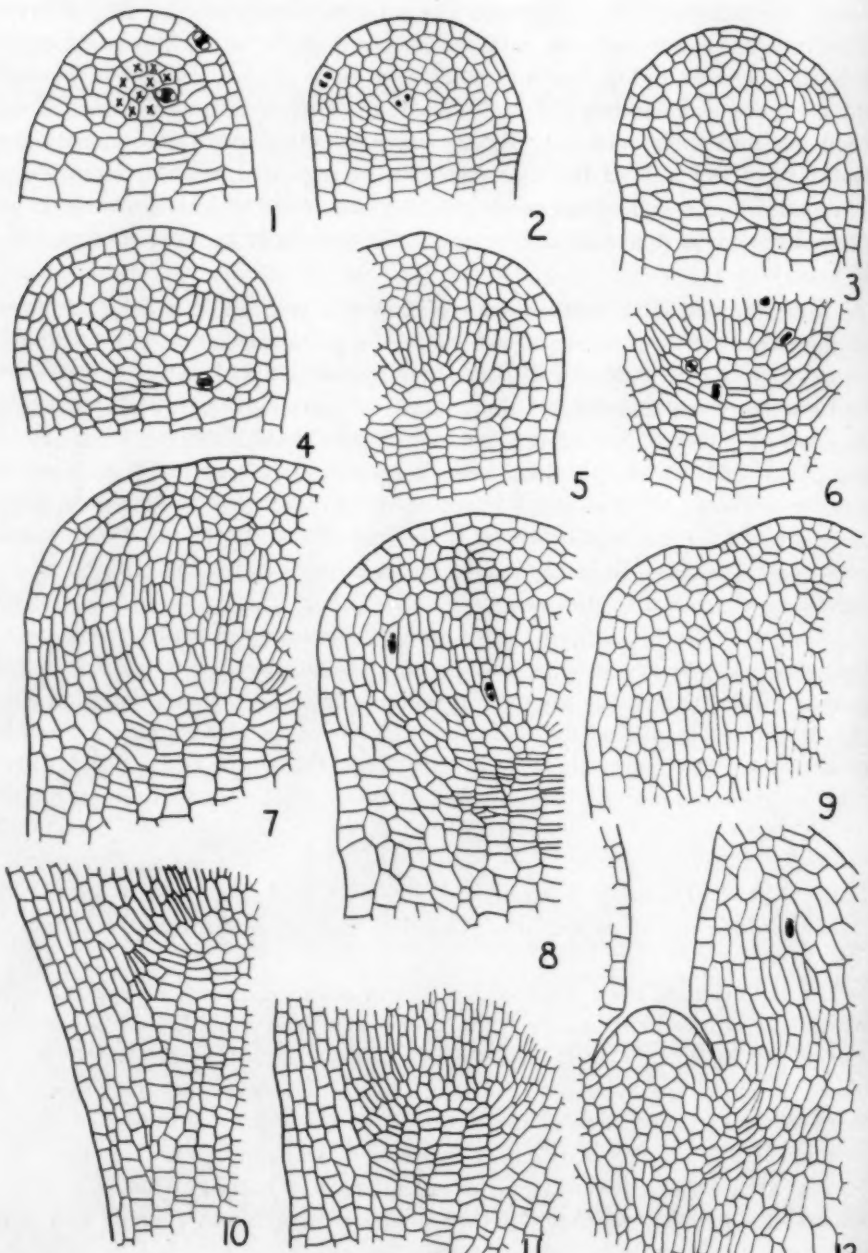
tween the parabolic free apex and the columnar suspensor of the embryo. The apical region consists mostly of small cells with deeply-staining, densely-granular cytoplasm and relatively large nuclei. In the suspensor, the cells are immediately distinct by virtue of their large size, their large vacuoles, and their relatively lightly stained cytoplasm. Consequently the majority of the cells of the free apex can be regarded as eumeristem cells. The cells of the initial region begin to stain slightly less intensely than their derivatives, but this difference is not especially marked at first (fig. 13).

Meristematic Differentiation. Within the free apex, a different type of development soon becomes noticeable. In an apparent extension of activity, a deeper center of cell division is produced within the eumeristem tissue a short distance below[2] the summit of the apex (figs. 1, 14, 21). Indicative of such an extension, some apices may show a different quality of cytoplasm in these deeper focal cells, somewhat reminiscent of the central mother-cell zone of the cycad shoot apex (Foster 1941). In this region, the cells stain more lightly than their immediate neighbors. Soon thereafter, the creation of a lower focal zone can easily be ascertained from the change in direction of new cell divisions (figs. 2, 21).

About the more lightly-staining area, particularly at its base and sides, the cells begin to divide with walls which are arranged in the direction of arcs of circles concentric about this region (figs. 2–4). Immediately within the area, the cells at first divide in variously oriented planes, with a seeming tendency for the new walls to lie in arcs about the center (figs. 2, 21). However, as growth proceeds, the cells within the central region divide in planes which are orthogonal to the longitudinal axis of the embryo, like Hanstein's (1868) "Würfelmeristem" or Schüepp's (1926) "massige Meristeme" (figs. 3–5). Towards the periphery of the zone, and immediately outside it, the concentric divisions spread outward to include a continually widening zone of cells.

There has thus been produced a lighter-staining group of central cells which are temporarily active. This group has been designated "stele promeristem" by Allen (1946), and the same term was used by the writer in the study on early embryogeny (Sterling 1948b). However, on the basis of a more critical examination of development in the *Taxus* embryo, the writer now prefers to employ a different expression. In view of the fact that this central area experiences only a limited amount of activity (hence is in the nature of a primary meristem rather than a primordial meristem) and only contributes indirectly to "stele" formation, and because it is located at the

[2] In the following descriptions, the free apex of the embryo (abmicropylar pole) is considered as its upper end and the admicropylar structures as toward the lower end.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"focus" (Sachs 1878) of various cell series, it might well be called a "focal zone." The organization of this temporarily meristematic region precedes the differentiation of the procambium and the root generative meristem (see below) in the conifer embryo.

At the free summit of the embryo, the superficial cells and the immediately underlying cells divide by anticlines and periclines, with anticlinal divisions predominating in the surface layer (figs. 3–5). The activity of these cells, which surmount the focal zone, becomes more limited, so that the volume of tissue contributed by their development is only a small percentage of the total at embryo maturity. At the time of organization of the central focal group, these cells above that group contribute to it to some extent. However, as the embryo enlarges, the surface initials become less and less active.

The concentrically dividing cells at the lateral boundaries of the focal zone are arranged early in a cup-shaped group, somewhat flared below the free apex of the embryo (figs. 4, 15, 16). As these cells divide, they become more densely staining than the cells external to them. In this early stage, they are also slightly more tabular. Since these cells possess the histological features of procambial tissue (and later develop the typical functions of that tissue), this bowl-shaped tissue may be referred to as procambium or procambial "cylinder."

Immediately outside the procambial zone, the adjoining cells also experience concentric divisions. In these more lightly staining cells, the new walls are oblique to the original anticlinal walls. Although the cells produced by these divisions enlarge to some extent, divisions occur more rapidly than restitution of cell volume. Thus arcs of narrow cells are produced, which have their greater diameter in the direction of the arc and a smaller diameter in the direction of the focal radius (figs. 3, 4). Inasmuch as the apparent size and shape of the mother cells is maintained initially, it is clear

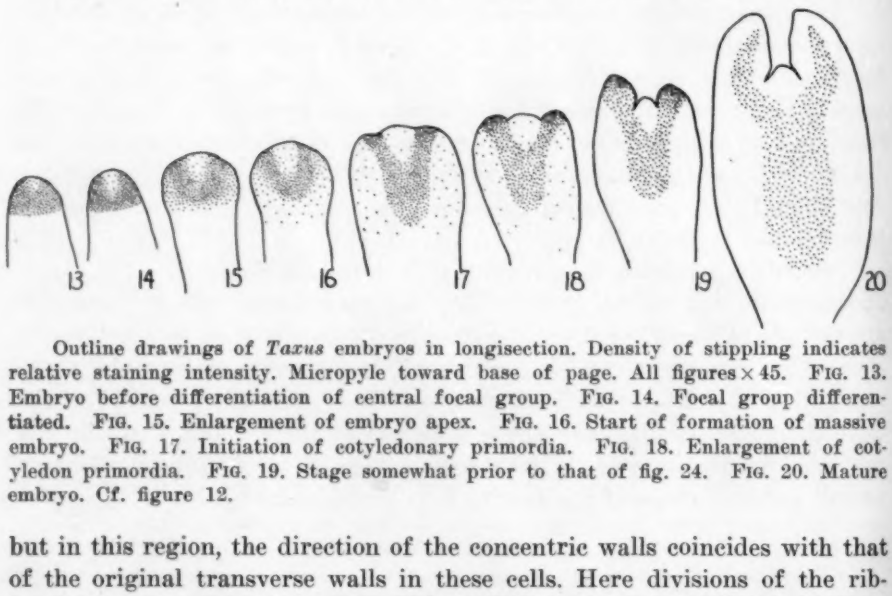
Explanation of figures 1–12

Camera lucida drawings of longisections of *Taxus* embryos, with micropyle toward bottom of page. All figures × 174. FIG. 1. Start of development of focal area below free apex. Focal cells indicated by "x." FIG. 2. Later stage, showing orientation of divisions about focal group. FIG. 3. Enlargement of cells in focal area, with indication of "Würfelmeristem" divisions here. Concentric divisions about focal group becoming marked. FIG. 4. Root generative meristem becoming active. Concentric divisions on lateral borders of core area are increasing the number of cortical layers. FIG. 5. Early start of formation of conical shoot apex in this embryo. Procambium becoming more distinct at sides of focal group. FIG. 6. Active root generative meristem in stage of about that of fig. 19. FIG. 7. Formation of buttress of presumptive cotyledon. FIG. 8. Procambial core becoming active behind root apical meristem. FIG. 9. Initiation of cotyledonary primordia. Note subepidermal activity. Shoot apex enlarging. FIG. 10. Region in vicinity of root generative meristem of large, near-dormant embryo. Absence of column and pericolumn is characteristic. FIG. 11. Region of root generative meristem of embryo in stage of fig. 29. FIG. 12. Shoot apex of mature embryo.

that the form of the daughter cells is not the direct result of a growth pressure by the central area.

Because cell divisions in the focal group occur in three orthogonal planes and since the newly formed cells here tend to enlarge to the size of the parent cells, the focal area enlarges, and its growth produces a swelling in the diameter of the embryo at the free apex (figs. 4, 5, 15, 16). The earlier-mentioned concentric divisions outside the focal region do not extend to the superficial layer of the embryo. Hence, as the internal tissue increases in volume, the outermost stratum accommodates to the increasing surface area by anticlinal divisions primarily. Few or no periclinal divisions occur in this superficial layer, so that its individuality is preserved (figs. 3–5, 7, 8, 26).

Below the focal area, tabular cells arranged in arcs are also to be found,



Outline drawings of *Taxus* embryos in longisection. Density of stippling indicates relative staining intensity. Micropyle toward base of page. All figures × 45. FIG. 13. Embryo before differentiation of central focal group. FIG. 14. Focal group differentiated. FIG. 15. Enlargement of embryo apex. FIG. 16. Start of formation of massive embryo. FIG. 17. Initiation of cotyledonary primordia. FIG. 18. Enlargement of cotyledon primordia. FIG. 19. Stage somewhat prior to that of fig. 24. FIG. 20. Mature embryo. Cf. figure 12.

but in this region, the direction of the concentric walls coincides with that of the original transverse walls in these cells. Here divisions of the rib-meristem type are numerous, and the cells have a very small longitudinal diameter in comparison with their transverse diameter (figs. 3–6, 21).

Just above this rib-meristem region, in the base of the focal area, is found a group of cells which remain slightly larger than their neighbors and slightly lighter-staining (figs. 5, 6, 8). Their large nuclei become prominent and noticeably spherical, but their chromatic material does not stain quite as intensely as that of the nuclei of adjoining cells. The group is further distinguished by the fact that its cells soon play the role of initial mother cells in the further development of the lower part of the embryo. Consequently, this region has been characterized by Schopf (1943) as gene-

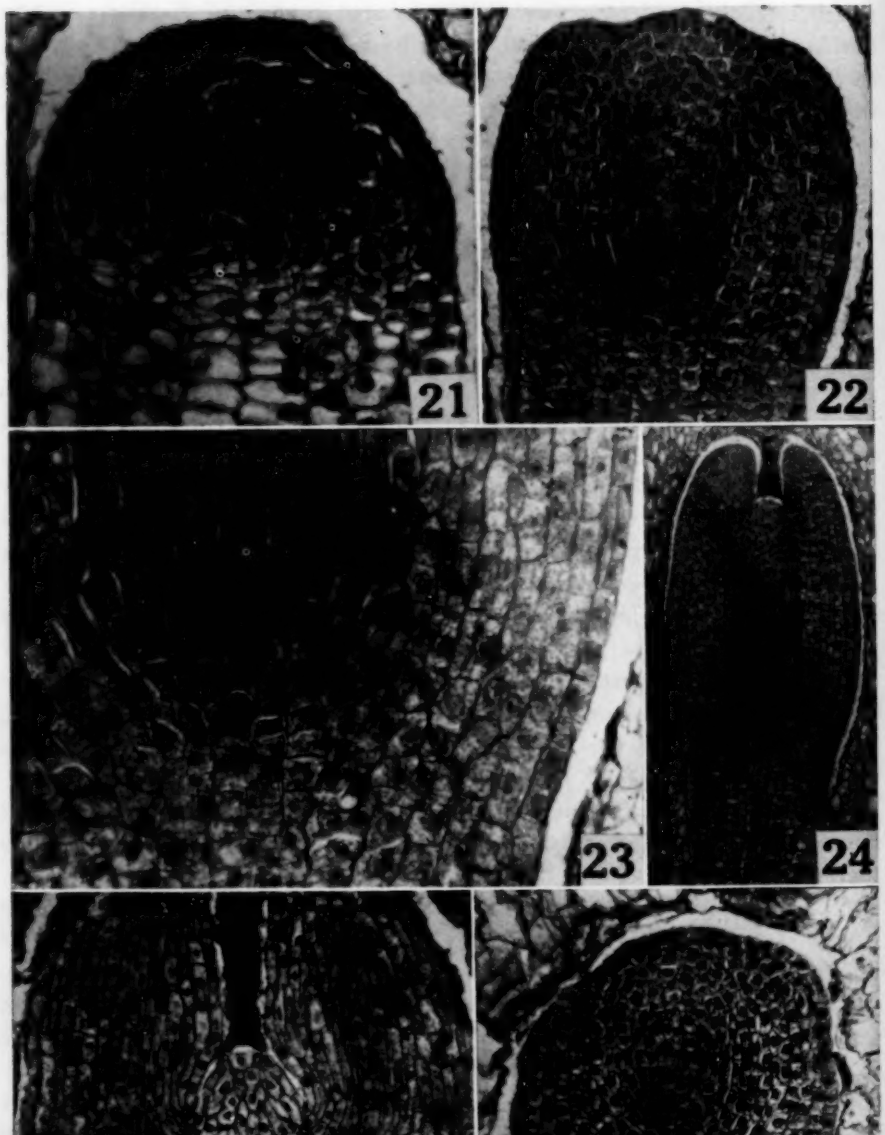
rative meristem and by Allen (1946) as root generative meristem. When developmental series are studied, it can be seen that this initial zone is differentiated in contact with the cylinder of procambium which has been formed on the sides of the focal region.

Production of the Massive Cylindrical Embryo. After the differentiation of the procambial cylinder and the root generative meristem, the suprasuspensor region of the embryo enlarges notably (figs. 7–9, 17, 18, 22, 26). The predominant increase in size occurs in the direction of the longitudinal axis. Just above the root generative initials, transverse divisions occur less rapidly than cell elongation, and longitudinal divisions in various planes become quite frequent. Hence, these cells become narrower and more elongate, remaining densely-staining as the surrounding cells begin to stain less intensely. In this manner, the cells of the lower part of the focal zone, just above the root generative meristem, acquire a definite procambial aspect.

These cells are the first procambial cells of the central core common to hypocotyl and root. They are formed in continuity with the procambial cylinder about the original focal group, being produced as the cells in the upper part of the focal zone become inactive. Between the two procambial zones, the region of juncture is V-shaped in longisection. Once formed, the procambial core experiences numerous longitudinal divisions, relatively fewer transverse divisions, and continuous cell elongation. Because of the future more or less autonomous growth of this central procambial strand, it might seem to deserve the name "stele promeristem" of Allen (1946). However, as a result of a critical examination of the stelar concept (Sterling 1949), it would seem more proper to designate the tissue in question as a procambial core, or simply procambium, as was done by Miller and Wetmore (1945).

At a slightly more advanced stage, the lower cells of the procambial core can be seen to converge definitely toward the initials of the root generative meristem. The arrangement of these cell lineages and of the division figures indicates the derivation of the lower procambial area from the root generative meristem (figs. 6, 26). That meristem can also be seen to give rise to many of the longitudinal files of cells in the young cortex immediately adjoining the procambium. In addition, the central rows and some more peripheral rows of suspensor cells obviously owe their origin to activity in the initials of this meristem.

The outermost layer of cells in the embryo exists as a discrete stratum (protoderm) below the flanks of the free apex, and it can be followed as such far down into the suspensor. Likewise, two or three hypodermal layers also appear to form a continuous, uninterrupted mantle (figs. 22, 26). These layers are perpetuated by anticlinal divisions mainly and are not re-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newed by the activity of the root generative meristem. However, occasional periclinal divisions may be seen in any of the young cortical layers, and the concentric divisions continue outside the upper part of the procambium to form additional cortical layers and thus increase the embryo diameter (figs. 7, 8).

As the procambial core region enlarges and elongates, a few more rows of cells are formed outside it in the cortex by the root meristem. The cells cut off along the lower edges of this meristem are shifted to the side by the continued advance of the meristem as well as by further lateral divisions in the meristematic cells. Consequently the new, centrally placed initials take over the meristematic function, and the more laterally situated ones (together with their derivative rows of cells) are displaced from the axial line to contribute to the embryonic cortex (figs. 6–8). Transverse divisions begin to occur more regularly in the displaced lineages as rib-meristem activity is initiated in the cortex.

Cotyledon Formation. As described above, the cells in the superficial layers of the embryo divide primarily by anticlines below the summit of the free apex. At the very summit, periclinal divisions are also frequent. Just below the apex, longitudinal divisions in the procambial cylinder and tangential divisions in the surrounding cortex, together with subsequent cell enlargement, produce an increase in embryo breadth. Thus broad shoulders are formed on the flanks of the free apex, and it is from these shoulders [equivalent to Louis' (1935) foliar buttresses] that the cotyledonary primordia are formed (figs. 7, 9, 17, 18, 22, 26). The two (or three) cotyledon emergences arise by active periclinal divisions in the hypodermal layer of cells at the buttresses. Although the surface layer may also undergo periclines, these seem far less significant than those in the subjacent layers in contributing to the volume of the emergence.

With regard to the procambial strands which supply these cotyledon primordia, it is interesting to note that there is here no question of acropetal or basipetal differentiation. As was pointed out above, the procambial cylinder is produced as a deeply-staining, cup-shaped zone following its initial differentiation. The upper edges of this cup rest against the flanks

Explanation of figures 21–26

Photomicrographs of longisections of *Taxus* embryos, with micropyle toward base of page. FIG. 21. Embryo just after differentiation of focal area. A few concentric divisions have occurred. ×312. FIG. 22. Initiation of cotyledonary primordia. Note continuity of deeply-staining cells from central procambium into cotyledon. ×152. FIG. 23. Root generative meristem of near mature embryo. ×312. FIG. 24. Near mature embryo. ×71. FIG. 25. Shoot apex of mature embryo. ×125. FIG. 26. Off median section of embryo which is forming cotyledonary buttresses. Flared upper edge of procambial region not shown in this view of edge of central procambium. ×152.

of the free apex of the embryo, and it is in conjunction with these regions of the procambial core that the cotyledonary primordia are initiated. Hence, the procambium of the embryonic body is blocked out as a unit before the formation of cotyledons and presages the future appearance of the latter (figs. 14–18).

At their first appearance, the procambial traces at the cotyledonary node are distinct only by virtue of their deeply staining cells and their more or less oblique course (figs. 19, 29). The enlargement of the cotyledonary primordia is attended by the elongation of the cells of their incipient bundles, so that the aspect of the latter becomes more and more definitely procambial, resembling closely the cells of the procambial core of the hypocotyledonary body (fig. 24). Outside the bundle, the cells of the cotyledons stain far less intensely and are more isodiametric than those of the procambium. Apical growth of the cotyledons continues in a small group of superficial initials which give rise to anticlinal and periclinal derivatives. The other surface cells of the cotyledons divide anticlinally alone, thus continuing the hypocotyledonary protoderm over most of the surface of the embryo.

Embryo Maturation. Once the various meristems have been organized and cotyledonary primordia produced, further development in the yew embryo involves pricipally an enlargement and a slight amount of further tissue differentiation in the different regions of the embryo. Although the cotyledons elongate somewhat, their length growth subsequent to their formation is not so great as that which takes place in the hypocotyl. Behind each growing cotyledon apex, a single procambial strand differentiates acropetally.

The embryo apex, which is a remnant of the original broader summit, may be considered as a minimal surface following cotyledon formation (figs. 12, 25). It is now definitely the shoot apex of the embryo. In this apex, the constituent cells stain far less intensely than the other cells nearby and are much larger and more isodiametric. Very little mitotic activity is displayed in this shoot apex of the maturing embryo. However, as the cotyledons enlarge and elongate, the shoot apex slowly enlarges to form a conical mound of tissue between them. Although no mitotic figures could be found in this growth, the increase in the number of cells indicates that some cell divisions have taken place.

Development in the hypocotylary region involves a great amount of cell division and elongation to produce the rather long body of the embryo. The procambial tissue in the center (figs. 23, 24, 28, 32) is composed of very narrow, elongated cells in rows which are traceable down to the root generative meristem. Divisions in the procambial core continue in the pattern followed before cotyledon initiation, viz., some transverse divisions and

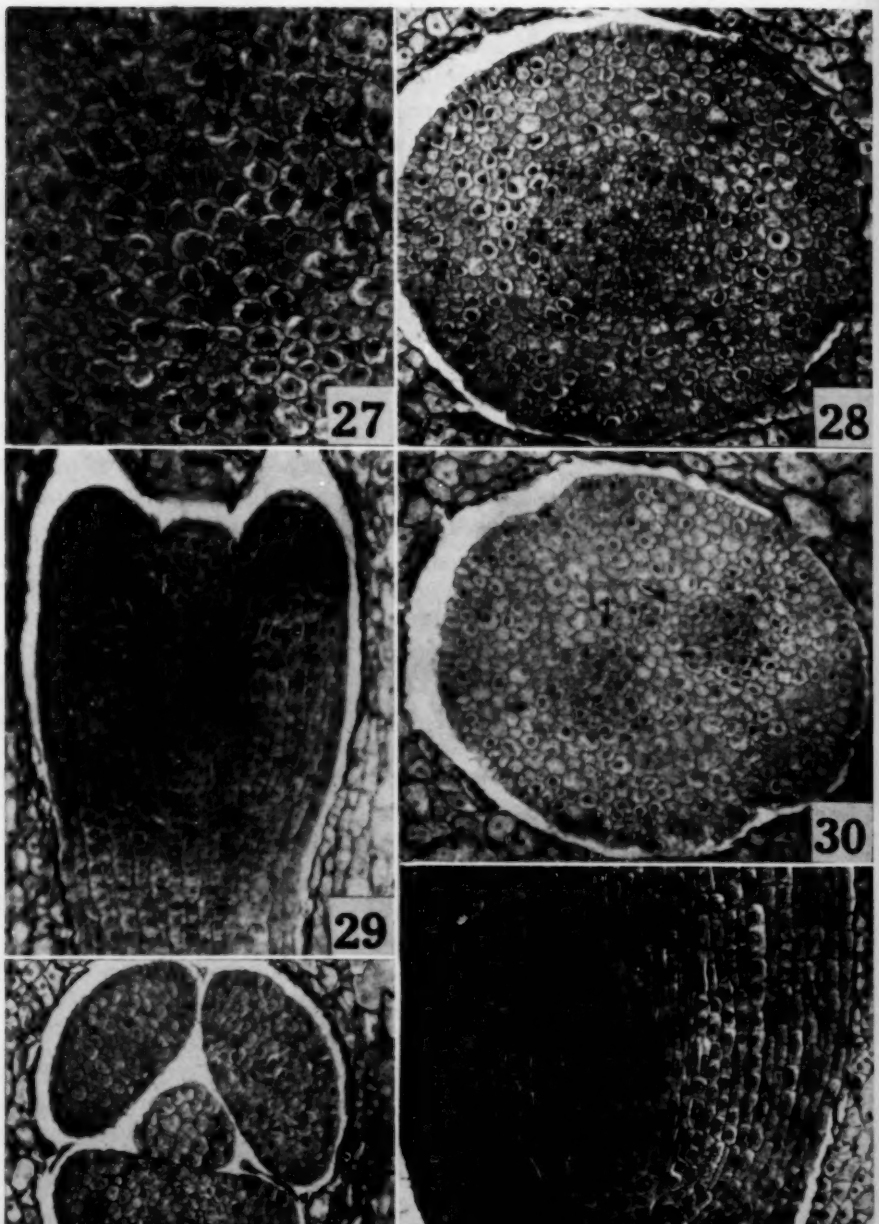
many longitudinal divisions in various planes. Thus, a cell which is cut off by the meristem toward the procambial area by a transverse division elongates in the long axis of the embryo and undergoes longitudinal divisions. Later, transverse walls may also be formed. Throughout the core area, these orthogonal divisions may take place at any distance from the root generative initials, so that the procambial core increases in volume autonomously.

However, those cells produced by the peripheral initials of the root meristem divide in a different fashion. In these cells, the subsequent divisions are more or less tangential. As the cell lineages are traced upward from the meristem, more and more tangential walls may be seen to be formed, increasing the number of cells at each successive level above the meristem—up to about four or five cells arranged in radial rows. The cells in these rows are intermediate in staining intensity between the cortical and the procambial cells. After germination, they may develop into so-called pericyclic tissue [said by Strasburger (1872) to consist of 2–5 rows of cells in the primary body of the root]. However, there are no precise divisions in the initials, nor does the subsequent ontogeny set off this region from the others produced by the root generative meristem. Even in a mature or almost mature embryo, these rows are definitely transitional between procambium and cortex in histology and mode of origin (fig. 23).

Since transverse divisions are relatively more numerous in the cortical area, the cells do not reach the length of the procambial initials. Occasional longitudinal divisions are to be noted in this stage of cortical development, but these are relatively rare in comparison with those transverse to the long axis of the embryo. Superficially, the rows of cortical cells appear to extend in lines continuous over the tip of the root generative meristem, but in actuality this configuration is due to the production of derivatives in radiating rows by the various initials of the root apical meristem and the gradual lateral displacement of these rows as the meristem advances and produces more of these rows of derivatives. Thus is created the "coaxial" pattern characteristic of a root apex.

Apparently the root generative meristem itself does not stand out very clearly. Its cells are arranged in a sort of horizontal disk, which is transverse to the longitudinal axis of the embryo (figs. 23, 27, 32). The initials are slightly larger than their derivatives, somewhat lighter-staining, and so situated that their derivatives can be seen to radiate out in all directions. Although divisions are not so frequent in the root generative meristem as in the cells cut off by it, they have been noted in fair abundance.

The root generative meristem furnishes cellular components not only for the body of the root but eventually also for most of the root cap–suspensor tissue. The suspensor is first produced by uniform rib-meristem activity behind the free apex of the young embryo (Sterling 1948b). Even after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the initial organization of the root generative meristem, the production of suspensor tissue (unlike that in the Pinaceae) follows this same pattern of uniform longitudinal rows of cells arranged parallel to the long axis of the embryo.

During the growth of the central procambial core, the activity of the root generative meristem in the admicropylar direction is not particularly marked. Consequently, as the procambial core enlarges, a difference in diameter becomes apparent between the hypocotyl and the suspensor. After the initiation of the cotyledon primordia, the activity of the root apical initials in the direction of the suspensor begins to increase slightly (figs. 10, 11, 32). In this manner, longitudinal rows of cells are produced directly below the meristem, seemingly set off more or less distinctly from those rows continuous between cortex and suspensor. However, the rows of root cap cells are rather short in comparison with the length of rows in that region in other conifer embryos, and they are not distinguishable from the suspensor proper.

The Mature Embryo. At maturity, the embryo does not differ markedly from its earlier appearance as described in the discussion of the maturing embryo. Suffice it to remark that the shoot apex is rather large, consisting of more or less isodiametric, lightly staining cells which appear to be inactive. Below this apex, a lightly staining region extends down a short distance into the procambium of the hypocotyl, perhaps as the equivalent of the more extensive medullary region of the pinaceous embryo (figs. 12, 20, 25). There is no definite pith, nor are secretory elements differentiated.

The two or three cotyledons (fig. 31) are relatively short, and their procambial strands (fig. 30) are strongly arched as they depart from the hypocotylary procambium (fig. 25). Neither in cotyledon nor in hypocotyl is there any vascular differentiation in the mature embryo. An epidermis is continuous over the mature cotyledons from the shoot apex to the hypocotyl, extending down over the hypocotyl as a uniseriate layer into the root cap-suspensor region (fig. 32). Several hypodermal layers also appear to exist as continuous strata between hypocotyl and suspensor.

Explanation of figures 27–32

Photomicrographs of *Taxus* embryos. In longisections, micropyle is toward bottom of page. FIG. 27. Cross section through root generative meristem of near mature embryo. ×208. FIG. 28. Cross section of hypocotyl of mature embryo about level of top of figure 32, showing central procambium. ×125. FIG. 29. Longisection showing enlargement of cotyledon primordia. Note how gametophyte tissue has been digested in advance of embryo. ×125. FIG. 30. Cross section near insertion region of the two cotyledons. The procambial strands are indicated by arrows. ×125. FIG. 31. Cross section through shoot apex of tricotyledonous embryo. ×125. FIG. 32. Lower part of near mature embryo, showing presence of several superficial cell strata continuous from hypocotyl to suspensor. ×125.

As in the prothallium, most of the cells of the embryo (with the exception of the procambium and the initial regions of root and shoot) are filled with ergastic contents, which are probably food reserves of some sort. It may be noted that while the initials of the root generative meristem are lightly-staining, they are neither as large nor as conspicuous as the shoot initials. The root apical initials are distinguishable from their derivatives only with difficulty in the mature embryo.

Surrounding the embryo is the large, pear-shaped mass of gametophyte tissue which has been enlarging simultaneously with the embryo. Development of this tissue appears to follow Jäger's (1899) description, with the multiplication of nuclei within its cells and further aberrant behavior, including fusion of these supernumerary nuclei. The cells of the gametophyte are large, multinucleate, and filled with spherical bodies of various ergastic materials. No microchemical tests were performed on the prothallial tissue to determine the nature of these cell inclusions.

Discussion. Attempts to explain the organization of a meristem in terms of the cell lineages which are a product of that organization can reach only a certain level of understanding. Such a level was virtually attained in the geometrical constructions of Sachs (1878, 1879). Although further refinements were introduced by Reinke (1880) and Schüepp (1926, 1946), their emendations have contributed more to a better analysis of the mechanics of growth than to an understanding of the causal factors in the organization of a plant meristem. However, it should be noted that, although describing meristematic activity in terms of cell lineages, both Sachs (1878, 1879) and Hanstein (1868) particularly stressed the fact that cell lineages were only a function of growth and organization in the meristem and not their determinant, that rather the inherent potentialities of the plant determined the patterns of cell division and cell elongation.

In his analysis of meristem structure, Sachs (1878) made a signal contribution which has been conspicuously neglected in later investigations. Sachs described the point about which anticlinal and periclinal cell rows were arranged as the common geometrical *focus* of these parabolic curves. Interestingly enough, this focal point was not always to be found among the initials themselves but sometimes lay deeper in the meristem, along its axis of growth. Coincidentally, in discussing the apical cell in cryptogams, Sachs showed that the focus lies in the apical cell itself and that this cell is the slowest-growing portion of the meristematic apex.

In addition to Sachs' observation, this phenomenon of diminished activity in a focal region may be seen to obtain in the apex of the root of *Angiopteris* (Schwendener 1882; Koch 1895). Similarly, the large-celled central mother cell group in the shoot apices of *Ginkgo* (Foster 1938) and the

cycads (Foster 1941) may be shown to be in the focal area. The same phenomenon appears in various conifer shoot apices (Sterling 1945, 1946) and root apices (Janczewski 1874; Flahault 1878; Schopf 1943), and recently Philipson (1947) has reported essentially this structure in the angiosperm shoot apex.

If it be accepted that the large size of the cells in a focal area reflects a diminution of meristematic activity (and perhaps growth also), a common quality seems to inhere in the apices of at least the gymnosperms and the lower tracheophytes. The apical meristems of root and shoot in these plants are alike in that the focus of growth (as defined by Sachs) is a region of minimal activity. The cell or cells in the focal area are generally larger than their neighbors, experience relatively fewer mitoses, and possess larger vacuoles in their cytoplasm. Their protoplasmic regions stain less intensely than those of surrounding cells, and their walls may be thicker. This anomaly of a functionally less active area as the central core of a developing meristem may be explicable in terms of diffusion gradients, oxygen supply, growth hormone production, hydrion concentration, etc. and perhaps also with respect to physical forces.

Immediately around the focal area the meristematic cells are smaller, thinner-walled, actively dividing, and have a higher nuclear-cytoplasmic ratio. This eumeristem tissue divides orthogonally with respect to the boundary of the focal zone, i.e., divisions in these cells are tangential and radial to the periphery of that zone. This tissue constitutes the segmentation zone of the lower tracheophytes and may be noted outside the focal zone in gymnosperm apices. Thus it is possible to visualize the focal region as a center of growth activity, from which cell lineages diverge in all directions and experience a more rapid mitotic activity than obtains in the cells of the focal region.

The organization of meristematic activity in the *Taxus* embryo appears to be based on the distribution of "focal zones." In this embryo, the differentiation of a central focal area below the free apex is related to the initiation of meristematic (and tissue) differentiation in further development. The cells above this zone (toward the free summit) continue as initials of the embryo shoot pole. The cells dividing laterally to this region constitute the precursor of the upper procambium and cortex; and the cells at the base of the focal zone initiate the body of the root and the root cap–suspensor tissue. As the cells in the upper part of the focal group become dormant, activity is continued in the lower cells of the zone, these cells becoming the initials of the root generative meristem. Such a relationship seems to occur also in the embryos of cycads (Guttenberg 1941) and *Ginkgo* (Lyon 1904; Sprecher 1907).

In connection with the zonal structure of the meristems in the embryo might be mentioned the phenomenon of procambial differentiation. Although the procambium in *Taxus* develops as a more or less central core of tissue which is continuous throughout the embryo axis at its initial differentiation (also *Phlox* of Miller & Wetmore 1945), Schopf (1943) describes it as appearing first at the node ("nodal meristem") in *Larix* and differentiating up into the cotyledons and down into the hypocotyl from that region. Likewise, Buchholz (1919) notes a late development of vascular strands after the start of cotyledon elongation in the pine embryo.

Despite the extensive comparative treatment of conifer embryogeny by Strasburger (1872) and Kapfer (1935), one or two features of the late embryogeny of *Taxus* justify a comparison with embryo development in other conifers. The most striking characteristic of the yew embryo is the relatively minor development of its root cap–suspensor region. This phenomenon was described in the embryo by Reinke (1873) and in the adult root by Strasburger (1872), Reinke (1873), and Janczewski (1874); it occurs also in the roots of *Cycas circinalis* (Reinke 1873), *Ginkgo* (Strasburger 1872), *Sequoiadendron* (Schwendener 1882), and *Biota* (Flahault 1878). In the *Taxus* embryo, the interesting feature of this limited development of the root cap is that, as a consequence, there are (1) series of continuous superficial cell strata extending from cotyledon into suspensor and (2) no "juncture zone" between the body of the root and the root cap, such as characterizes the pinaceous and cupressad embryos (Strasburger 1872; Buchholz & Old 1933; Kapfer 1935; Cook 1939; Schopf 1943; Allen 1947; Wang 1947).

Soon after the differentiation of the root generative meristem in the Pinaceae, there occurs a remarkable, virtually *autonomous* development (as described by Reinke 1872 and Kapfer 1935) in the root cap–suspensor region to form a "column" and "pericolumn" (Schopf 1943). Only after this development has been initiated, does the hypocotylary region begin to elongate. In fact, in *Keteleeria* (Wang 1947) there appears to be little or no subsequent enlargement of the hypocotyl despite the extensive growth of the root cap–suspensor. On the other hand, in *Taxus* the development of the hypocotyl is continuous upon the differentiation of the root generative meristem. Only later is the root cap region formed by this meristem, and this cap constitutes a minor portion of the embryo, consisting of but a few longitudinal cell rows. Kapfer (1935) describes the very narrow root cap–suspensor but fails to mention the continuous protoderm.[3]

On the whole, the pinaceous embryo is characterized by the presence of

[3] Apparently a "rhizodermis" (Allen 1947) develops with regular root activity, which involves the sloughing off of the root cap and the outer layers of the cortex (Strasburger 1872).

a pith and secretory elements (Hutchinson 1917; Buchholz & Old 1933; Kapfer 1935; Schopf 1943; Allen 1947; Wang 1947). Although Kapfer has reported resin canals in *Taxus baccata,* neither these nor a pith could be detected in the embryo of *T. cuspidata.* The yew embryo agrees with all conifer embryos heretofore studied in the presence of a relatively large, rather inactive shoot apex, in the manner of origin of the different tissue regions of the embryo, and in the nature of growth of the root generative meristem. Generic differences may occur in the number of vascular strands which supply the cotyledons, but within certain limits, the total number of strands and of cotyledons formed appears to be a matter of nutritional relationships, whose effect is also expressed in embryo size (Hill & de Fraine 1913; Buchholz 1946).

SUMMARY

Meristematic development and tissue differentiation is described in the embryogeny of *Taxus cuspidata.* After apical growth has occurred for some time in the young embryo, the differentiation of a focal area of lighter-staining cells just behind the apex foretokens the formation of the root generative meristem and procambium. The focal area enlarges, and adjacent cells divide with walls concentric about this area. Simultaneously, the root generative meristem becomes active, furnishing abmicropylar cells which contribute to the formation of hypocotylary procambium and admicropylar cells which contribute to cortex and suspensor.

As the focal group becomes less active, the cells produced by the lateral concentric divisions build up buttresses of tissue on the flanks of the free apex of the embryo. Deeply-staining cells in these buttresses have a histological continuity with the cells of the elongating procambial core of the hypocotyl. Although later cotyledon growth occurs by activity of superficial initials, cotyledonary primordia are raised from the buttresses by predominantly subepidermal activity. The procambial strand in each cotyledon, always continuous with the procambial core, develops acropetally behind the apex of the cotyledon.

Only after marked hypocotyl elongation and cotyledon enlargement does the root generative meristem produce any tissue resembling the "column" of the pinaceous root cap. This tissue is very indistinct, and as a consequence of this type of development, there is no "juncture zone" on the outer surface of the embryo, and the epidermal layer and several hypodermal layers are continuous from the cotyledons into the suspensor.

As in other conifer embryos, the shoot apex is a conical mass of apparently dormant cells, which are large and have a lightly-staining cytoplasmic matrix. The ripe embryo lacks vascular and secretory elements, and

no pith is present. The cotyledons, usually two in number (sometimes three), are relatively short.

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CASPARIAN STRIPS IN ISOETES MACROSPORA

DOUGLAS W. DUNLOP

In longitudinal and cross section through the stem and leaf base region of *Isoetes macrospora* Dur., stained with crystal violet-iodine, the cells of the ligule are found to contain stored material which is greater in amount than in other parts of the plant.

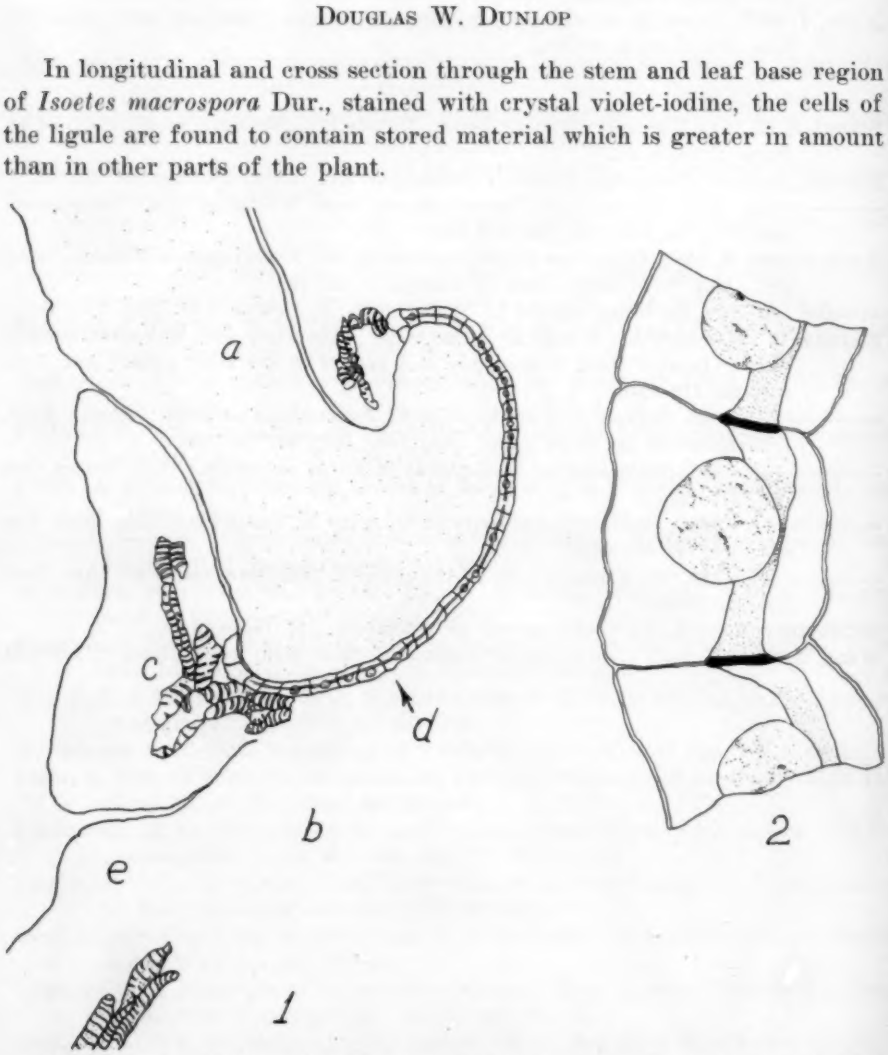

FIG. 1. *Isoetes macrospora* Dur. a, ligule. b, leaf base. e, velum and vascular tissue. d, endodermal-like layer. e, region of sporangium initials. FIG. 2. Enlarged view of endodermal-like cells showing casparian strips.

A superficial layer of cells of the leaf (fig. 1, d) is conspicuous lining the cavity in which lies the imbedded part of the ligule (fig. 1, a). The cells

of this layer are smaller than the adjacent leaf cells and in general are rectangular in sectional view. The radial walls of each cell of the layer possess casparian strips (fig. 1, d), and in section the layer closely resembles the endodermis of some angiosperm roots.

The function of these endodremal-like cells with their casparian strips is not clear, although the difference in amount of deposit and the location of the tissue would suggest that the endodermal-like layer may be involved in the concentration of materials in the ligule.

Similar unequal deposition of material was observed in *Selaginella rupestris* (L.) Spring. where at fairly early stages of development the ligule appears relatively free of stored material, but as development proceeds most of the cells stain heavily, whereas in tissue of leaf, stem, and sporangium adjacent to the ligule the stain is light so that contrast between the ligule and adjacent tissue is marked.

Here as in *Isoetes macrospora* there is a modification found in the leaf cells that ensheath the ligule base. Early in their development the protoplasts of the elongate sheath cells deposit a casparian-like, but less conspicuous, strip on their radial walls.

CONCLUSIONS

1. True casparian strips are present in cells of a specialized layer of the leaf at the ligule base of *Isoetes macrospora*.

2. Groups of tracheids are found in contact with the endodermal-like layer that ensheaths the ligule base.

3. Histologically the endodermal-like layer of *Isoetes* and the endodermis of some angiosperm roots might reasonably be compared.

4. Evidence of physiological similarity is insufficient.

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AN ADDITIONAL REPORT ON THE GROWTH OF EXCISED TOMATO ROOTS

WILLIAM J. ROBBINS AND MARY STEBBINS

The excised tomato roots isolated September 29, 1935, and maintained in culture since that time are now in their 144th passage. For the last 131 passages one set of roots has been maintained in a solution limited to mineral salts, cane sugar, and thiamine. Another set was maintained in a solution of mineral salts, cane sugar, and thiazole.

The present paper reports results on the relation of temperature and age of inoculum to the beneficial effect of pyridoxine and the present status of the roots which have been continuously cultivated in solutions supplemented with thiazole.

Temperature and the Effect of Pyridoxine. We have demonstrated earlier that pyridoxine improves the growth of this strain of tomato roots provided there is present in the medium an adequate supply of thiamine. Our strain of tomato roots is unable to synthesize thiamine. When thiamine is supplied, growth is limited because of the inadequate amount of pyridoxine synthesized by the root from the basal constituents of the medium. The addition of pyridoxine to the medium containing thiamine results in a substantial increase in growth. We do not know what limits growth in solutions containing both thiamine and pyridoxine. This strain of roots does not respond to nicotinic acid.

Our present concern was to determine whether differences in incubation temperature materially affected the response to pyridoxine.

In a preliminary experiment, roots incubated at 30° C did not survive. We therefore chose 15°, 20°, and 25° C as the temperatures of incubation. Roots were grown individually in 150 ml. Erlenmeyer flasks in 50 ml. of modified Pfeffer's solution containing 1 per cent cane sugar and supplemented with 10 mμ moles of thiamine and 50 mμ moles of pyridoxine. Details of the preparation of the solutions have been given earlier.

Each treatment was replicated 15 times and carried out in two series. For one series, the inoculum was obtained from passage 122 in thiamine solution when that passage was 28 days old. The roots in this series were allowed to grow at the three temperatures for 57 days, removed, washed with distilled water, dried at 100° C for 24 hours and weighed. For another series, the inoculum was obtained from passage 123 in the thiamine solution when the passage was 41 days old. Dry weights of the roots in this series were determined after 30 days growth.

Growth in the solutions containing thiamine and pyridoxine was 2–4 times that in the thiamine solutions at 15°, at 20°, and at 25° C (fig. 1). Although growth at 15° C was quite slow, the beneficial effects of the pyridoxine were quite definite.[1] A temperature of 25° C was somewhat better than 20° C for growth in the solutions supplemented with thiamine and in those supplemented with thiamine and pyridoxine. The heaviest

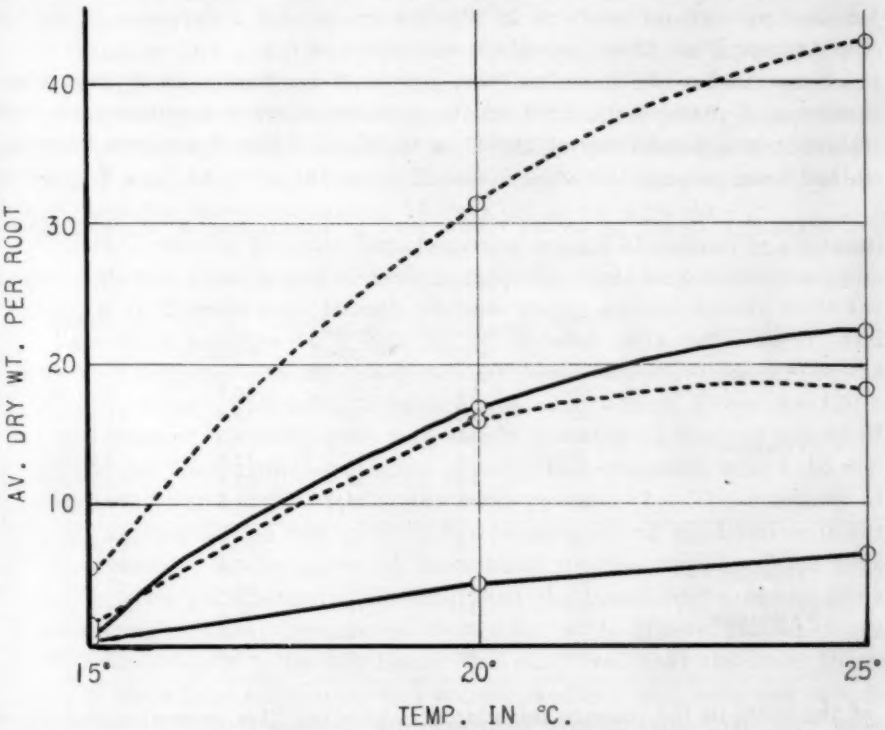

FIG. 1. Average dry weights of tomato roots grown in mineral salts and 1 per cent cane sugar at 15°, 20° and 25° C; solid line below, for 30 days in solutions supplemented with thiamine; solid line above, for 57 days in solutions supplemented with thiamine; dotted line below, for 30 days in solutions supplemented with thiamine and pyridoxine; dotted line above, for 57 days in solutions supplemented with thiamine and pyridoxine.

root weighed 55.8 mg. and was grown in 57 days at 25° C in the solution supplemented with thiamine and pyridoxine. The heaviest root in the solutions supplemented with thiamine weighed 24.1 mg. The weights were greater at the end of 57 days than at the end of 30 days.[2]

[1] For roots grown 57 days, the average dry weight at 15° C in the thiamine solutions was 1.4 mg.; in the solutions supplemented with thiamine and pyridoxine, it was 5.6 mg.

[2] Roots allowed to grow for several months at 20° C in the dark in 50 ml. of Pfeffer's solution with 1 per cent cane sugar and 10 mμ moles of thiamine have reached average weights of 60 to 80 mg. For example, 28 roots averaged 80.9 mg. after 7 months.

In the experiment described, inoculum 28 days old was used in one series and in the other the inoculum was 41 days old. Does the age of the inoculum affect the final dry weights?

Age of Inoculum. To determine whether the age of the inoculum appreciably affected the final dry weights obtained in solutions supplemented with thiamine or with thiamine and pyridoxine, an effort was made to obtain inoculum as uniform as possible except for differences in age in the passage from which inoculum was obtained.

Some 44-day-old inoculum was prepared by transferring root fragments on September 21, 1946, to the nutrient solution supplemented with thiamine and incubating at 20° C in the dark. These fragments were obtained from passage 126 when it was 39 days old. After 44 days, fragments

TABLE 1. *Growth of excised tomato roots of various ages in solutions supplemented with thiamine or thiamine and pyridoxine.*

Supplement	Temp. ° C.	Age of Inoculum Days	No. of Roots Weighed	Av. dry wt. mgm.	Range mg.
Thiamine	20	14	15	15.1	9.0–20.2
	20	32	15	18.8	11.8–27.7
	20	44	15	24.5	18.7–39.7
	25	14	15	11.1	7.1–19.1
	25	32	15	21.1	11.3–28.6
	25	44	14	20.7	13.0–28.3
Thiamine and Pyridoxine	20	14	14	30.7	21.3–44.8
	20	32	14	35.6	22.3–50.1
	20	44	15	36.0	27.9–47.6
	25	14	15	37.7	31.5–65.1
	25	32	14	44.5	32.2–54.0
	25	44	15	38.5	19.5–75.2

of the roots in the passage inoculated September 21st were transferred to the nutrient solution containing thiamine and to the solution supplemented with thiamine and pyridoxine. Some of the flasks were incubated in the dark at 20° and some at 25° C.

The 32-day-old inoculum was obtained by transferring on October 23, 1946, fragments of some of the roots of September 21st to solutions supplemented with thiamine or with thiamine and pyridoxine and incubating at 20° and at 25° C.

The 14-day-old inoculum was obtained by first inoculating thiamine solutions on October 21st with root fragments from the cultures of September 21, 1946. The cultures of October 21st were then used on November 4th as inoculum for the thiamine series.

In the procedures outlined above, the passages from which the 14-, 32-, and 44-day-old inoculum was obtained were all inoculated with fragments

of excised roots which had grown for approximately 1 month in a thiamine solution at 20° C in the dark.

Each treatment was replicated 15 times, and the roots were grown at 20° and 25° C in the dark for 2 months.

Growth (dry weights) obtained from the 14-day-old inoculum was consistently less than that from the 32- or 44-day-old inoculum (table 1). The differences were least marked at 25° C in the solutions supplemented with thiamine and pyridoxine, and most marked in the solutions supplemented with thiamine only. This suggests that as an excised root grows in a thiamine solution, it slowly accumulates something which favors later growth of its fragments when they are transferred. This material did not reach its maximum in 14 days. However, pyridoxine was beneficial no matter whether the inoculum was 14 days old or 44 days old.

Roots Grown in Medium Supplemented with Thiazole. We reported earlier[3] that at times it was difficult to maintain roots in a solution supplemented with thiazole only, though we have grown excised tomato roots for 105 successive passages in a solution of mineral salts, cane sugar, and thiazole. Beginning with the 116th passage (96th successive passage in the thiazole solution), increasing difficulty was experienced. From the 120th to 126th passage, the roots grew very slowly reaching an average weight of about 3.0 mg. even after 4–6 months growth. This compares with 6–16 mg. in 2 months during the 84th to the 96th passage (1). The slowness of growth was not due to any error in the preparation of the basal nutrient solution because the series in the same basal solution supplemented with thiamine grew satisfactorily. We suspected the possibility that the stock thiazole might have decomposed but tests with *Mucor Ramannianus* showed the thiazole to be functional. We concluded that the roots themselves in their long cultivation had become modified and were less able to grow in the Pfeffer's solution supplemented with thiazole than they were originally.

We considered that these roots might have lost the ability to synthesize pyrimidine. However, when roots which had been continuously cultivated in solutions supplemented with thiazole were transferred to solutions containing thiamine, little improvement in growth occurred although three successive transfers were made in the thiamine solution.

SUMMARY

The strain of excised tomato roots which has been maintained for 144 passages, each approximately 1 month in length, grew slowly at 15° and more rapidly at 20° or 25° C; 25° C was somewhat superior to 20° C.

[3] **Robbins, William J.** A report on the growth of excised tomato roots. Jour. Arnold Arb. **27**: 480–485. 1946.

The roots could not be maintained at 30° C. Pyridoxine was beneficial in the presence of thiamine at all three temperatures. Excised roots which had grown 14, 32, and 44 days in a particular passage were used as inoculum. Pyridoxine was beneficial for all three types though consistently lower dry weights were obtained with the youngest inoculum. Roots which had been grown for 96 successive passages in a solution supplemented with thiazole proved difficult to maintain. Some change in their metabolism apparently took place which made them difficult to cultivate in solutions supplemented with thiazole or thiamine.

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TORREYA

PROCEEDINGS OF THE CLUB

Minutes of the Meeting of April 6, 1948. The meeting was called to order by President Small at 8: 05 P.M. at Columbia University; 75 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. Barbara McClintock of the Carnegie Institution of Washington, Cold Spring Harbor, New York, spoke on "The relation of a gene-controlled breakage of a chromosome to the general problem of genic instability."

The meeting was adjourned at 9: 40 P.M.

Minutes of the Meeting of April 21, 1948. The meeting, at Hunter College, was called to order by President Small at 8:40 P.M.; 25 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. M. A. Johnson, of Rutgers University, spoke on "The Shoot Apex in Vascular Plants." His abstract follows:

> The structure and organization of the shoot apex in vascular plants was described and compared. The apex in the lower forms is either dominated by a master apical cell or by a group of initials which contribute to the tissues of the shoot. Both conditions may occur in a single genus, as in *Selaginella*. The cycads have an apical, superficial, initiating layer but their apices are noteworthy for their striking zonation; two prominent features are a central region of mother-cells and an active, flanking, meristematic mantle. In the higher gymnosperms the apices are not only smaller but fail to show the degree of zonation seen in the cycads. Periclinal divisions are less frequent in the superficial layer, especially at the tip of the apex. They appear to be entirely absent both at the tip and in the flanks of the apex of *Gnetum* except during leaf initiation. The angiosperms possess apices with two rather distinct zones; an outer consisting of one or more layers of cells—the tunica—which increases in area, and an inner core—the corpus—which increases in volume. The problems in deriving the angiosperm shoot apex from the gymnospermous types were discussed. Further evidence is required before more than tentative conclusions can be reached. It is possible, however, to arrange a more complete intergrading series between the gymnospermous and angiospermous types of shoot apex than was formerly supposed to exist.

The meeting was adjourned at 9: 50 P.M. Refreshments were afterwards served in the laboratory by the Hunter College department of botany.

Minutes of the Meeting of October 20, 1948. The meeting was called to order at Columbia University by President Small at 8: 15 P.M.; 24 members and friends were present. Dr. P. P. Pirone of The New York Botanical Garden gave an illustrated discussion of "Some Important Diseases of Shade Trees." His abstract follows:

> Shade trees, like all living things, are subject to several highly destructive fungus and virus diseases. Perhaps the most important fungus disease in the present century, which was largely responsible for making the public "tree conscious," is the chestnut blight.
>
> Another, though perhaps not so destructive one, is the Dutch elm disease which has destroyed thousands of fine elms in the northeastern United States in the past fifteen years.

Of more recent origin, and more destructive than either of the two, is the virus disease of American elm known as phloem necrosis. Thousands of large elms in Columbus, Ohio, alone have succumbed to this disease in the last few years. One vector for this disease has recently been determined as the leafhopper *Scaphoideus luteolus*. Tests are now under way to determine whether DDT applications will control the leafhopper and thus check the spread of the disease.

The London plane (*Platanus acerifolia*), often incorrectly referred to by nurserymen as the Oriental plane, is subject to several highly destructive fungus diseases.

The first is cankerstain, first found near Philadelphia and now occurring over a wide area, which is highly fatal. Infection usually occurs through man-made wounds. Spread from diseased to healthy trees also occurs through use of contaminated pruning saws, poles, and other arborist's equipment.

Apparently new to science is the *Dothiorella* canker disease, still largely confined to the metropolitan New York area. Nearly fifty confirmed cases have been found within the past year and all have been disposed of by burning to check further spread.

The minutes of the preceding meeting were read and approved. The meeting was adjourned at 9: 15.

Minutes of the Meeting of November 17, 1948. The meeting was called to order at 8: 05 P.M. by President Small at Hunter College; 42 members and friends were present. Dr. Michael Levine, of Montefiore Hospital, spoke on "Growth and Differentiation of Plant Tissues in vitro." His abstract of the address follows:

Intercalary meristem of the tap root of *Daucus carota*, and of stems of *Helianthus annuus*, *Nicotiana Langsdorffii*, *N. affinis*, *N. tabacum*, *N. glauca*, and *N. glutinosa*, was grown aseptically on synthetic media to which 0.6 per cent of well mashed shredded agar-agar was added. Growth of these tissues was increased by the addition of 0.5 mg. per cent of indole acetic acid or less of α-naphthalene acetic acid. The chemical carcinogens, 1,2,5,6-dibenzanthracene, 3,4-benzpyrene, or 20-methycholanthrene, were added in varying concentrations to the media to determine the effect of these agents on these tissues. The meristem of the carrot root gave rise to three types of tissue masses. The nodular tissue mass was characterized by pigmented globular masses from which there occasionally appeared a sparse distribution of roots. The whole mass assumed an inverted cup-shaped form and in a medium with one of the growth substances or a chemical carcinogen this tissue in section presented the appearance of crown gall, "plant cancer." Cultures of the thalloid form were pale green in color and consisted of thallus-like bodies, broad-tipped and tapering at the base. These bodies were composed of parenchymatous tissue with irregular strands of vascular elements. Under the influence of the chemical carcinogens the epidermal cells in these organized bodies proliferated and formed numerous buds of embryonal tissue. These differentiated and formed abortive and normal plantlets.

The hyaline or third type of tissue mass was the most common form following the use of heteroauxin. It was yellowish-brown in color and produced an abundance of roots. This tissue mass transferred to media with one of the carcinogens or a standard substrate produced completely differentiated plantlets typical of the carrot. Roots and leaves of these cultures grown on low concentrations of indole acetic acid de-differentiated and formed hyaline tissue masses.

Segments of stems of *N. Langsdorffii* and *N. affinis* formed tissue masses in consistency not unlike those of the hyaline tissue masses of the carrot. Fully differentiated plantlets have grown from these tissues. Stem segments of *N. tabacum* produced surface proliferation and formed buds from the meristem which developed stems, leaves, and finally roots. These reactions are unlike those in the carrot.

The factor responsible for the differentiation of the tissue masses into complete plantlets are not conclusively established. Indole acetic acid in culture media facilitates growth, induces changes in tissue organization; roots are formed. Its influence on differentiation of stem tissue may be indirect. The chemical carcinogens used in these experiments produce malignant growth in animals. In these studies evidence of growth, stimulation, hyperplasia, bud formation, and complete differentiation occur in their presence. Factors needed to convert normal cells into malignant growths seem to be lacking in the plant.

The meeting was adjourned at 9: 15 for refreshments served by the Hunter College botanists.

Minutes of the meeting of December 2, 1948. The meeting was called to order at 8:15 P.M. by President Small at Hunter College; 50 members and friends were present. Dr. Rudolf Florin of the Hortus Bergianus, Stockholm, spoke on "The Telome theory in its Application to the Reproductive Organs of the Cordaites, Conifers, and Taxads." His summary follows.

According to the telome theory (W. Zimmerman 1930, 1938, 1945) the transformation of the simple organization of the earliest vascular land plants of the Upper Silurian and the Lower and Middle Devonian formations into the more complicated organization of the geologically-younger tracheophytes, including those of the present time, is the result of a few principal organogenetic processes running their course more or less independently, viz. overtopping, planation, fusion, reduction and recurvation. The overtopping of a uniform truss of dichotomizing telomes (and mesomes) leads to its differentiation into an axis and lateral organs, the latter with a primary alternate arrangement. The planation implies a change of the primary cruciate dichotomy into flabellate dichotomy, i.e. the telomes (and mesomes) are brought into the same plane. The fusion connects telomes (and mesomes) either by parenchyma alone ("webbing") or, in addition, by the steles of the telomes (and mesomes). The various types of steles have arisen by fusion from the protostelic condition of the earliest vascular plants. Reduction of an overtopped telome system may ultimately lead to the formation of a simple uninerved leaf. Recurvation of telomes occurs particularly in fertile organs.

The telome theory is of interest in connection with the problem of the evolution of the reproductive organs in the cordaites, conifers, and taxads. The radial, repeatedly dichotomized sporangial trusses of the earliest vascular plants—with terminal erect sporangia—are a primitive type from which, according to this theory, all sporangial trusses of the tracheophytes derive. There is a large gap between this primitive condition and that represented by the organization of the Upper Carboniferous cordaites, which have radially symmetrical fertile dwarf-shoots or flowers arranged in inflorescences and constituting much transformed lateral mixed telome systems. The female flower is composed of an axis carrying spirally disposed

bifurcated leaves (telome trusses) or simple leaves (telomes), and ovule-bearing megasporophylls (sporangial trusses). But these axillary, partly fertile dwarf-shoots of the cordaites have retained primitive features, such as the radial symmetry, the spiral arrangement and dichotomous branching of the leaves and megasporophylls, and the terminal position of the sporangia. At the apices of the megasporophylls the mesomes became aggregated, so that three telomes arose from the same point of furcation: two lateral vegetative telomes forming the integument and one terminal fertile telome (sporangium).

The more reduced of the two cordaitean types of female flowers known so far leads directly to the *Lebachia* type of the earliest conifers from the Upper Carboniferous and Lower Permian formations. The megasporophyll of *Lebachia* with its single, terminal, erect ovule entirely corresponds to that of the later cordaites and may therefore also be assumed to derive from a dichotomized truss of terminal naked sporangia. The integument has the same nature as in the cordaites.

In the conifers the sporophylls and sterile scales on the axis of the female flower soon changed from the primitive spiral to a decussate arrangement by rhythmically repeated reduction of mesomes. Further, the anterior part of the flower was suppressed, and the sporophyll became strongly reduced and incorporated in the sterile part of the flower, so that finally the ovule appears to be seated directly on the surface of this so-called ovuliferous scale.

The female flowers of the taxads differ from those of the true conifers by not being arranged in inflorescences and by the absence of lateral fertile telome systems on the floral axis. The uppermost of the overtopping branches of the whole primary telome system, from which the flower derives, was a fertile telome or sporangium. Consequently this became placed terminally on the floral axis itself. The integument appears to be formed out of two or more vegetative aggregated telomes—or in certain cases, telome systems—which constitute overtopping lateral branches of the floral axis. In position, each of these telomes or telome systems corresponds to a whole sporangial truss (megasporophyll with several ovules or, after reduction, one single ovule) in the cordaites and conifers.

While the structure of the female cones of *Lebachia* apparently derives from that of the inflorescences of the cordaites, their male flowers differ considerably. In the earliest conifers, the floral axis carries exclusively microsporophylls in its fertile region, which are moreover hypopeltate, hyposporangiate, and bisporangiate, while in the cordaites the microsporophylls are intermingled with sterile scales and terminated by clusters of 4–6 erect sporangia. In the earliest conifers, the male flowers are placed singly and terminally on branchlets, while in the cordaites they are united into inflorescences. The primitive nature of the cordaitean microsporophyll is evident from its branching by cruciate, isotomic dichotomy. It derives from an undifferentiated telome system with terminal sporangia, which was subjected to reduction of its upper mesomes and to flattening of the basal mesome, so that the microsporangia became seated at the tip of a uninerved sporophyll, just as the ovule is.

The microsporophylls of the conifers and taxads represent more advanced stages than those of the cordaites. The taxads have radially sym-

metrical or dorsiventral microsporophylls, in one genus intermingled with sterile scales. The peltate, perisporangiate microsporophyll of *Taxus* appears to be the more primitive in this group and to derive from a dichotomized telome system with terminal erect sporangia. This conception implies the assumption that the peltate, perisporangiate organization is a transitional stage in the course of the organogenetic development, which led to the confinement of the sporangia to the abaxial side of the sporophyll. In the later true conifers, as in *Lebachia*, the axis of the male flower always carries exclusively sporophylls in the fertile region; these are moreover dorsiventral, hyposporangiate, and bisporangiate to plurisporangiate. They probably also derive from radial, undifferentiated, and dichotomizing sporangial trusses, with terminal erect sporangia. The conifers differ from the taxads, however, in that the peltate, perisporangiate stage in the organogenetic development of the microsporophyll seems to have been absent.

After extended discussion, the meeting was adjourned at 10: 20. No business was transacted. Refreshments were served by the staff of Hunter College.

Minutes of the Annual Meeting, January 5, 1949. After dinner at Hunter College the annual meeting was called to order by President Small at 8:10 P.M.; 76 members and friends were present.

The minutes of the four preceding meetings (at which no business was transacted except for the reading of papers) were read in summary and approved.

The following were elected to membership in the Club: Honorary Life Member: George T. Hastings, Santa Monica, Calif. Active Members: Don S. Bolley, Brooklyn, N. Y.; Richard S. Cowan, New York, N. Y.; Albert W. Cross, Palo Alto, Calif.; Samuel J. Golub, Springfield, Mass.; Seymour Hutner, New York, N. Y.; Ivar Jorstad, Oslo, Norway; Pauline F. Kayser, Brooklyn, N. Y.; Edwin B. Kurtz, Jr., Tucson, Ariz.; Irwin E. Lane, Honolulu, Hawaii; Barbara McClintock, Cold Spring Harbour, N. Y.; Robert B. Platt, Emory University, Ga.; Richard A. Popham, Columbus, Ohio; Harry Thiers, College Station, Tex.; Associate Members: Augusta Allen, Allenwood, N. J.; Louis Lichtenberg, Newark, N. J. Three resignations were received with regret.

Mr. Vernon L. Frazee was appointed chairman of the Field Committee.

Dr. Simpson reported on the activities of the Program Committee, announcing the discontinuance of the afternoon meetings and adoption of the practice of holding two evening meetings a month. As chairman of the Exchange Committee Dr. Simpson reported that the Bulletin is at present exchanged for 22 publications.

Dr. Lawton gave a preliminary Treasurer's report which included the information that income for the past year had exceeded both estimates and expenditures by about $500; that $2,700 was available from past surpluses for the publication of the seventy-five-year Index of the Bulletin; and that the endowment fund amounted to somewhat more than $26,500; that the club had 731 members of whom about 540 were Active Members; and that there were about 300 paying subscribers to the Bulletin. The President announced that Mr. Peloubet and Dr. Hammond would serve as Auditing Committee.

Dr. Camp presented for Dr. Rickett the report of the editor of the Bulletin. It was pointed out that Volume 75 included 750 pages, and this unusual size was made possible by the subsidization of 115 pages; that the number of articles submitted was increasing, to the point where it may be difficult to have publication keep pace with the authors; that the cost of publication is approaching $10 a page (compared to $5.25 in 1940); and that studies had been undertaken of more economical means of publication. Dr. Camp reported also that 74 of the 75 published volumes of the Bulletin had been indexed.

Dr. Matzke reported on his duties as delegate to the New York Academy of Sciences and for the Andrews Fund Committee, and Dr. Small for the Local Flora Committee.

Dr. Clum, as Business Manager, reported a net income from back numbers of the Bulletin, the Memoirs, the Index, and Torreya, and from advertising in the Bulletin, of $1213.38.

Dr. Levine reported on the activities of the Membership Committee.

Dr. Seaver's report for the Budget Committee consisted of the following: Estimated Income—$7500.00; Estimated expenses—Bulletin publication, $5500.00; Advertising $275.00; Torreya reprints, $150.00; Index cards, $275.00; Bibliographer's honorarium, $150.00; Treasurer's office, $200.00; Treasurer's honorarium, $150.00; Business Manager, $200.00; Corresponding Secretary's office, $125.00; Recording Secretary's office, $25.00; Editor's office, $50.00; Membership committee, $150.00; Field Committee, $200.00; General expenses, $50.00; Total, $7,500.00. It was moved, seconded, and carried without dissent that this budget be adopted for 1949.

Dr. Small reported, as delegate to the New York and New Jersey Trail Conference, on the preparation of a guide-book to the local segment of the Appalachian Trail. He also gave an account of a meeting concerning the destruction of the swamp in Van Cortland Park, and the proposed formation of a Conservation Council of Greater New York. It was moved, seconded, and carried without dissent that a committee be appointed to formulate a resolution protesting the transforming of the swamp into a part of a golf-course. It was also moved, seconded, and carried without dissent that the Club participate in the proposed Council, there being no appropriation authorized by this action.

Dr. Simpson reported, for the tellers, that the mail ballots had selected the following officers for the Club: President, Edwin B. Matzke; 1st Vice-president, Charles A. Burger; 2nd Vice-president, Marion A. Johnson; Corresponding Secretary, Jennie L. S. Simpson; Recording Secretary, Donald P. Rogers; Treasurer, Elva Lawton; Editor, Harold W. Rickett; Business Manager, Harold H. Clum; Bibliographer, Lazella Schwarten; Representative on Board, N. Y. Botanical Garden, Rutherford Platt; Delegate, N. Y. Academy of Science, Michael Levine; Representatives, A.A.A.S., P. W. Zimmerman, Ralph H. Cheney; Members of the Council, L. M. Black, P. P. Pirone, Norma E. Pfeiffer, George S. Avery.

It was moved that the nominations be closed and the Secretary directed to cast one ballot for the persons named; the motion was seconded and carried without dissent, and the officers declared elected.

After the business meeting, which adjourned at 9:10, Dr. Small gave his address as retiring President on the activities of the Field Committee for the past ten years; his account was illustrated with colored slides, made on various field trips of the Club.

Respectfully submitted,

DONALD P. ROGERS,
Recording Secretary

NOTES

Two new biological periodicals deserve mention. *Hydrobiologia*, subtitled *Acta hydrobiologica, limnologica et protistologica*, is published at The Hague. The first issue reached New York in October, 1948. It contains articles on dangerous algae from the United States and from South Africa, on phytoplankton of the Mediterranean, on photosynthesis in the phytoplankton, besides several taxonomic papers. Authors are from Michigan, Cape Town, Barcelona, Switzerland, Holland, Budapest, Praha, and Zagreb. The table of contents is followed by the titles announced for the next issue, with a similar international group of authors.

Vegetatio, subtitled *Acta geobotanica*, also published in The Hague, is the official

organ of the Association Internationale de Phytosociologie. It also includes papers in a variety of languages, by botanists of France, Switzerland, Holland, Spain, and Palestine.

Such evidence of international cooperation in science is encouraging, and it is to be hoped that these publications will have an enthusiastic reception.

Review

The Evolution of Gossypium and the Differentiation of the Cultivated Cottons. By J. B. Hutchinson, R. A. Silow and S. G. Stephens. i–xi, 1–160, *f. 1–10* + *pl. 1–9*. London: The Oxford University Press. 1947.

With the closing of the Genetics Department, Cotton Research Station, Trinidad, B.W.I., a notable era in the advancement of cotton research was terminated. We are indebted to Hutchinson, Silow and Stephens for combining the results achieved by the investigators at the Cotton Research Station with the work of Harland in Peru, and of Beasley, Kearney and Webber in this country, into an extremely interesting and lucid description of the evolution of the cotton plant.

The book is divided into four parts. Part One, "The classification of the genus *Gossypium*," is by Hutchinson; Part Two, "The evolution of the species of *Gossypium*," is by Hutchinson and Stephens; Part Three, "The differentiation of the true cottons," is by Hutchinson and Silow; and Part Four, "The significance of *Gossypium* in evolutionary studies," is by Hutchinson and Stephens. These separate parts are not a series of disconnected essays as one might expect, but a well-digested account of the factors contributing to the evolution of a genus, unique by the fact of its long historical association with man.

There is general agreement among cotton investigators in regard to the main facts that emerge from this work.

1. The species of *Gossypium* may be conveniently segregated into three groups: (a) the wild species (n = 13 chromosomes) found in both Old and New Worlds; (b) the Old World cultivated cottons (n = 13); (c) the New World cultivated cottons (n = 26). An important exception is the Hawaiian tetraploid cotton, *G. tomentosum* Nutt. It appears to be a truly wild species, and genetically it is closely related to the New World cultivated cottons.

2. Independent genetic and cytological evidence indicates that the New World cultivated cottons are allotetraploids with one genome homologous with that of the Old World cultivated cottons, while the other genome is homologous with that of the wild American species. Evidence derived from experimentally produced allopolyploids points to the probability that the Old World cultivated ancestor was *Gossypium arboreum* L., or a close relative. The nearest living ancestor of the American wild species appears to be *G. raimondii* Ulb., a wild species from the coast of Peru.

3. The wild, lintless species of *Gossypium* have a wide geographic distribution in the tropics and subtropics of both hemispheres. This is not true of the individual species, which for the most part are narrowly restricted in distribution. They are xerophytic, perennial shrubs, genetically well separated, and of low intraspecific variability. According to the authors, "Judging from the wild species, *Gossypium* is a stationary or receding genus made up for the most part of ancient relic species."

4. On the other hand, the cultivated cottons are an aggressive group. As a result of their close association with man, they have found congenial habitats within a wide belt of the earth's surface in tropical and subtropical lands. This success is evidently based on two characters, namely, the convoluted lint hairs, and the annual habit. Each character is comparatively simple genetically but the change (i.e. from lintless to linted) has involved the entire reorganization of the genotype, through the accumulation of gene differences.

The chief area of controversy concerns the *time* at which the American cultivated allotetraploids originated. Harland has suggested that the ancestral species were brought together over a Pacific land bridge in late Cretaceous or Tertiary times. The present authors have developed a number of serious objections to this theory that appear to make it untenable.

Recently Stebbins[1] has advanced a suggestion that does away with the necessity of the Pacific land bridge portion of Harland's theory. He assumes that hybridization between the parental genomes occurred in North America, probably during the early part of the Tertiary period. From this center the allopolyploids spread southward, as well as out into the Pacific Islands. "With the cooling of the climate in the middle of the Tertiary period, all except certain of the New World diploids disappeared from North America, but the tetraploids survived in South America and perhaps also on the West Indies." This proposal clears away some of the objections to Harland's theory, but certainly not all of them.

Hutchinson and Stephens, in contrast to Harland, believe that the New World allotetraploids are of comparatively recent origin. They suggest that the Asiatic cultivated cottons were carried by an ancient civilization across the Pacific, to the mountain valleys of northwestern South America, where natural hybridization of the cultivated crop with a neighboring wild species (presumably *Gossypium raimondii*) produced the first allotetraploid. There are a number of pieces of evidence, biological, ethnological, and archeological, which when fitted together form a rather consistent picture in favor of the theory of recent origin. However, none of the evidence, if considered independently, is decisive. The chief stumbling block is the negative and highly speculative nature of the argument for the crossing of the Pacific from Polynesia to South America by an ancient culture.

In their zeal to support the recent origin theory by trans-Pacific migration the authors are guilty of a minor error. They have listed *Cucurbita* as having two Old World centers of origin. *Cucurbita* is strictly a New World genus; there is not the slightest evidence of any species being endemic in the Old World.

Students of evolution will be interested in the stimulating discussion of the development of new characters and the significance of polyploidy. The chapter on the evolutionary prospects of a crop plant will be illuminating to those whose studies have been confined to non-domesticated species.

The quality of the paper, the printing, and binding are exceptionally good for these times. The photographs, line drawings, and maps are well reproduced. There is a list of approximately 160 references, and three separate indexes (I, Index of names of species, varieties and races of *Gossypium;* II, Index of authorities quoted; III, General index).

Finally, in planning research with crop plants, administrators of agricultural programs in this country might well follow the example set by the far-sighted policy of the Empire Cotton Growing Corporation. This little book of 160 pages is proof of the wisdom of including fundamental botanical and genetic studies in a crop research program.—THOMAS W. WHITAKER.

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[1] **Stebbins, G. L., Jr.** Evidence on rates of evolution from the distribution of existing and fossil plant species. Ecol. Monogr. **17**: 149–158. 1947.

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

ALGAE

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(See also under Phytopathology: **Allington: Gorenz, Walker & Larson**)

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